

For Reference

NOT TO BE TAKEN FROM THIS ROOM

Ex LIBRIS
UNIVERSITATIS
ALBERTAENSIS



For Reference

NOT TO BE TAKEN FROM THIS ROOM

UNIVERSITY OF ALBERTA

A STUDY OF PURPLE MARTINS AT THE NORTHERN
LIMIT OF THEIR BREEDING RANGE.

by



JAMES CAMPBELL FINLAY

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE
STUDIES IN PARTIAL FULFILMENT OF THE
REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

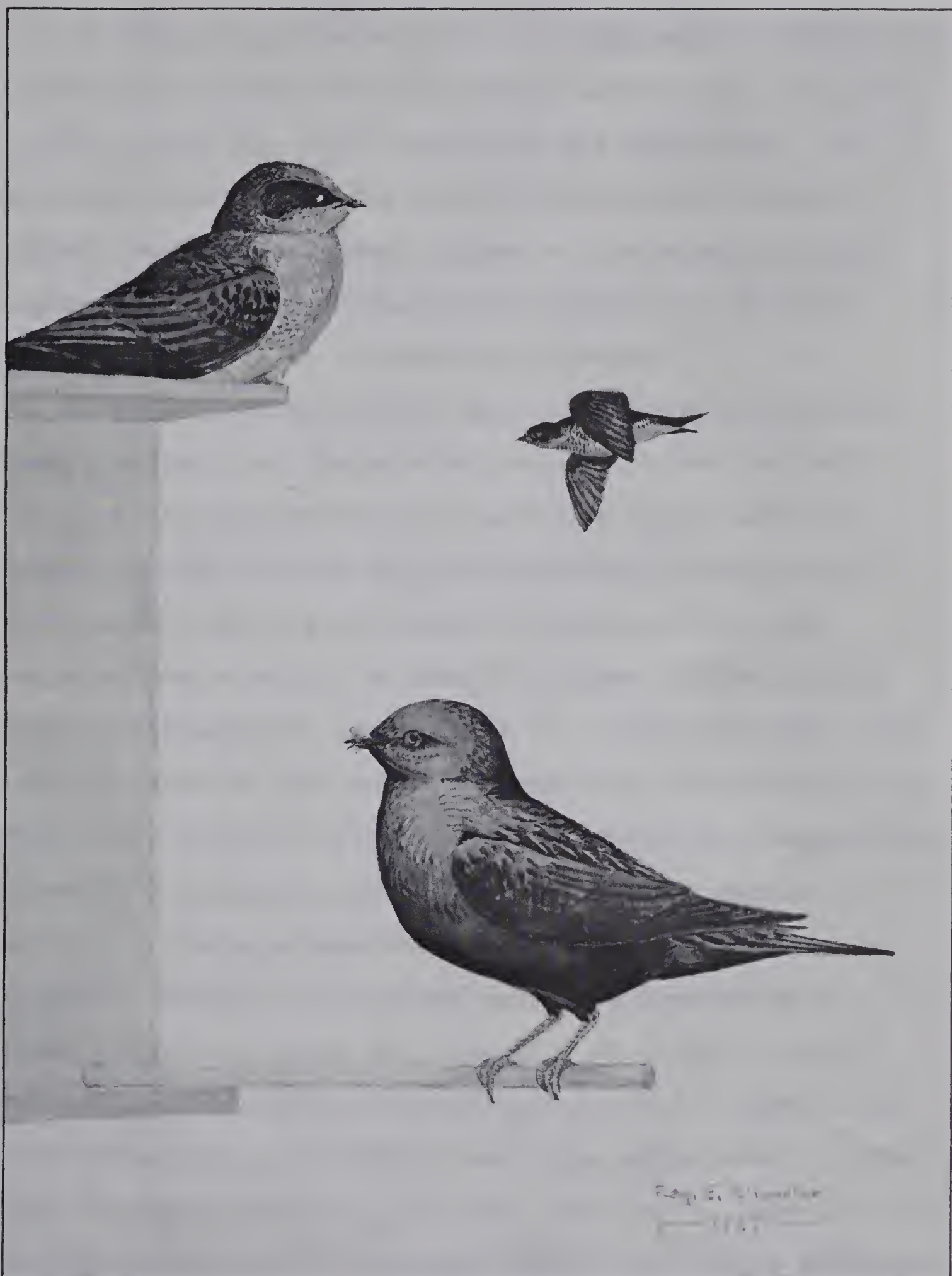
EDMONTON, ALBERTA

SEPTEMBER, 1968

THESIS
1968(F)
66

UNIVERSITY OF ALBERTA
FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read,
and recommend to the Faculty of Graduate Studies for
acceptance, a thesis entitled A Study of Purple
Martins at the Northern Limit of Their Breeding
Range, submitted by James Campbell Finlay in
partial fulfilment of the requirements for the
degree of Master of Science.



ABSTRACT

A study of purple martins was undertaken to examine the influence of several meteorological factors upon one phase of their activity - nest entrances and departures - and to determine the characteristics of this bird's breeding biology near the northern limites of its breeding range. Research was conducted during the summers of 1965 and 1966 in the vicinity of Edmonton, Alberta.

Certain weather factors were correlated with purple martin activity at the nest entrance. It was assumed that correlations during the "nestling stage" were indirect, acting through the availability of aerial insects which form the majority of purple martin food. Correlations outside the "nestling stage" reflected the relative strength of territorial vs. feeding drives. Rain lasting three or more hours substantially reduced activity. When other factors were studied in combination temperatures below 55°F were most influential on recorded martin activity. Temperatures above about 59°F had little influence. Martin activity was generally greater on a clear to partly cloudy day than on a dull day. Wind velocities above about 6.5 mph, particularly above 15 mph reduced activity. Relative humidities above about 65 percent tended to decrease activity. Barometric pressure per se and barometric pressure changes had little influence on purple martin activity at the nest entrance. Of the seven stages in the breeding cycle, activity during the nest completion stage was influenced most by weather, and

activity during the incubation stage was influenced least. It appeared that average weather conditions at Edmonton were not limiting productivity of purple martins. Their increase at this latitude probably is limited by nest site availability.

The breeding cycle was divided into seven stages. These stages and the mean duration of each were: arrival, nest-cavity defence and pair-bond formation - 6.5 days; nest building - 11.8 days; nest completion - 3.2 days; laying - 4.8 days; incubation - 16.6 days; nestling - 27.4 days; post-breeding defence of nest cavity - 5.9 days. Clutches laid later in the season were smaller. The number of young fledged varied from one to seven with a mean of 3.4 for 55 nests. These breeding statistics are not significantly different from those reported by Allen and Nice (1952), except that incubation was longer, and fledging success greater at the latitude of Edmonton. During the nestling stage activity at the nest entrance, presumably reflecting the rate of feeding of nestlings, increased to day 10, was maintained through day 13, and decreased after day 14. As brood size increased, the nest entrance and departure activity decreased per nestling. Males in adult plumage were observed to feed young at a rate similar to females, whereas males in first nuptial plumage fed young at half this rate. Males in first nuptial plumage were the main participants in the post-breeding defence of the nest-cavity.

ACKNOWLEDGMENTS

I wish to acknowledge my indebtedness to my committee members for their guidance throughout the execution of this study: to Dr. D.A.Boag for his continued encouragement and constructive criticism of the manuscript; to Dr. J.S.Hayward for his suggestions and valuable criticism of the thesis; and Dr. H.O. Hohn for his advice and criticism of the manuscript.

I must also express my thanks to the many people who offered their services and opinions for my benefit: Mr. Robert Lister who, over the years, continued to encourage me to pursue further knowledge; Dr. W.A.Fuller for his early encouragement and loan of several pieces of equipment; Dr. K.W.Smilie, Department of Computing Science, for his generous assistance in the statistical analyses employed; Mr. R.W.Longley, Department of Geography, for his advice in weather systems; the staff of the University of Alberta Technical Services Section, for their efforts in designing and building the electronic equipment, particularly Mr. D. Malensky; Mr. J. Sheratt of Canadian Electronics Ltd. for his technical advice on electronics; Mr. A. Mann of the Meteorology Branch of the Department of Transport for providing meteorological instruments, weather data and answering numerous technical questions; Mr. G.H.W.Ashley for building special bird houses; Mr. R. Chandler for

drafting all the figures, and many hours of profitable discussion; Mr. A. Porcher for some of the 1965 photographs and Mr. A. Karvonen for the 1966 pictures; Mrs. Leslie Lin (née Dawson) for field assistance; Brett and Warren Finlay whose small hands provided access to nestlings in cavities inaccessible to me; Mr. A. Porcher who in 1965 so generously provided his garage and yard for the equipment and his time to assist in data collection and several years' banding operations; Messrs. J. Easterbrook, W. Salamandik, J. Lothamer, F. Skinner, and W. M. Leisman, all of whom provided access to their backyard colonies in 1965; and the many colleagues in the Department of Zoology who offered their services and opinions for my benefit.

My gratitude to my wife, Joy, is boundless for her encouragement throughout the project. While I studied and wrote this thesis over the past four years she cheerfully took over responsibilities we previously had shared, managed the family affairs, and looked after the household and our three children. The task would not have been completed without her eternal optimism and cooperation on the home-front.

I was supported during the summer of 1965 with a grant from the R. B. Miller Biological Station Fund. The Department of Indian Affairs and Northern Development, National Parks Branch, provided a site for the 1966 research and allowed me time both summers to collect data. I gratefully acknowledge these benefactors.

Chapter 1: Introduction

Chapter 2: Introduction

Chapter 3: Introduction

Chapter 4: Introduction

Chapter 5: Introduction

Chapter 6: Introduction

Chapter 7: Introduction

Chapter 8: Introduction

Chapter 9: Introduction

Chapter 10: Introduction

"There is really no such thing as
bad weather, only different kinds
of good weather."

JOHN RUSKIN

"Quoted by Lord Avebury"

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION.	1
PROCEDURE	3
RESULTS AND DISCUSSION.	11
INFLUENCE OF WEATHER.	11
Rainfall	17
Temperature.	20
Sky Opacity.	27
Wind Velocity.	31
Relative Humidity.	35
Barometric Pressure.	38
Multiple Weather Factors	42
REPRODUCTIVE CYCLE AND PRODUCTIVITY	53
Arrival, Nest-Cavity Defence and Pair-Bond Formation	54
Nest Building	57
Nest Completion	59
Laying	62
Incubation	70
Nestling	72
Post-Breeding, Nest-Cavity Defence	83
GENERAL DISCUSSION AND CONCLUSIONS.	88
LITERATURE CITED.	92

APPENDIX I	Nest boxes used in 1965 to collect data on purple martin activity at the nest entrance.	103
APPENDIX II	Three of the four purple martin nest complexes used in 1966 at Elk Island National Park.	104
APPENDIX III	One of the photo-electric and mechanical switch unit boxes which were attached to each nest box to record the number of nest entrances and departures by purple martins in 1965.	105
APPENDIX IV	Circuit diagram of the 1965 and 1966 electronic set-up used for measuring the number of nest entrances and departures by purple martins in the Edmonton region.	106
APPENDIX V	Meteorological instruments used to collect data at Elk Island National Park in 1966.	107
APPENDIX VI	Purple martin activity at the nest entrance during the nestling period as influenced by two meteorological factors in combination, one factor being barometric pressure.	108
APPENDIX VII	Purple martin activity at the nest entrance as influenced by the two factors: temperature and sky opacity.	109
APPENDIX VIII	Purple martin activity at the nest entrance as influenced by the two factors: wind velocity and sky opacity.	110
APPENDIX IX	Purple martin activity at the nest entrance as influenced by the two factors: temperature and wind velocity.	111

APPENDIX X	Purple martin activity at the nest entrance as influenced by the two factors: wind velocity and relative humidity.	112
APPENDIX XI	Purple martin activity at the nest entrance as influenced by the two factors: sky opacity and relative humidity.	113
APPENDIX XII	Purple martin activity at the nest entrance as influenced by the two factors: temperature and relative humidity.	114
APPENDIX XIII	Purple martin activity at the nest entrance during the arrival, nest-building and nest completion stages of the breeding cycle as influenced by the three factors: temperature, sky opacity and wind velocity. . . .	115
APPENDIX XIV	Purple martin activity at the nest entrance during the laying, incubation, nestling and post-breeding stages of the breeding cycle as influenced by the three factors: temperature, sky opacity, and wind velocity.	116
APPENDIX XV	Purple martin activity at the nest entrance during the arrival, nest defence, pair-bond formation stage as influenced by four factors: temperature, sky opacity, wind velocity and relative humidity. . . .	117
APPENDIX XVI	Purple martin activity at the nest entrance during the nest building stage as influenced by four factors: temperature, sky opacity, wind velocity and relative humidity. . . .	118
APPENDIX XVII	Purple martin activity at the nest entrance during the incubation stage as influenced by four factors: temperature, sky opacity, wind velocity and relative humidity. .	119

APPENDIX XVIII Purple martin activity at the nest entrance during the nestling stage as influenced by four factors: temperature, sky opacity, relative humidity and wind velocity. 120

APPENDIX XIX Measurements of adult purple martins from the Edmonton area compared to birds in the Eastern United States. 121

LIST OF TABLES

Table 1.	A comparison of purple martin ED activity recorded mechanically and observationally over 3-hour periods in 1966.	11
Table 2.	Comparison of mean ED activity with that recorded while rain fell during the different stages of the breeding cycle of purple martins.	17
Table 3.	The relationship between purple martin activity at the nest entrance and temperature during the major divisions of the breeding cycle.	21
Table 4.	Influence of temperature upon ED activity in the post-breeding nest-cavity defence stage of the purple martin breeding cycle.	23
Table 5.	Influence of temperature upon ED activity in the arrival, nest defence, pair-bond formation stage of the purple martin breeding cycle.	24
Table 6.	Mean temperatures over many years at Edmonton and in the rural surroundings for the months of May to August inclusive.	26
Table 7.	The relationship between purple martin activity at the nest entrance and sky opacity during the major divisions of the breeding cycle.	28
Table 8.	The relationship between purple martin activity at the nest entrance and wind velocity during the major divisions of the breeding cycle.	32
Table 9.	The relationship between purple martin activity at the nest entrance and relative humidity during the major divisions of the breeding cycle.	36

Table 10.	The relationship between purple martin activity at the nest entrance and rising and falling barometric pressure during the major divisions of the breeding cycle.	39
Table 11.	The relationship between purple martin ED activity during the separate divisions of the breeding cycle and meteorological factors taken in combinations of two.	43
Table 12.	A second method of analyzing the relationship between purple martin ED activity during the separate divisions of the breeding cycle and meteorological factors taken in combinations of two.	44
Table 13.	The relationship between purple martin activity at the nest entrance during separate divisions of the breeding cycle and meteorological factors taken in combinations of three including temperature, sky opacity and wind velocity.	47
Table 14.	A second method of analyses of the relationship between purple martin activity at the nest entrance during separate divisions of the breeding cycle and meteorological factors taken in combinations of three including temperature, sky opacity and wind velocity.	48
Table 15.	Distribution of time periods required for the nest building stage in the breeding cycle of purple martins in 1965 and 1966 at Edmonton, Alberta.	57
Table 16.	Distribution of time periods for the nest completion stage by purple martins in the Edmonton area.	59
Table 17.	Weekly comparison of the termination of nest building and nest completion stages for purple martins at Edmonton, Alberta.	60

Table 18.	Distribution of purple martin clutch sizes in the Edmonton area, Alberta.	65
Table 19.	Clutch size in purple martins, in relation to the onset of laying in the Edmonton area, Alberta.	66
Table 20.	Distribution of time periods for the duration of incubation for purple martins in the Edmonton area, Alberta.	71
Table 21.	Distribution of time periods for the nestling stage in purple martins at the experimental boxes in the Edmonton area, Alberta.	72
Table 22.	Distribution of time periods prior to the appearance of nestlings at the nest entrance.	76
Table 23.	A comparison of purple martin productivity at Edmonton, Alberta with that reported at three colonies in the U.S.A., as reported by Allen and Nice (1952).	78

LIST OF FIGURES

- Figure 1. Record of purple martin ED activity taken from a 20-channel Esterline Angus recorder. 5
- Figure 2. Average hourly ED activity of purple martins for three days in each of the stages of the breeding cycle from arrival to nest completion. 8
- Figure 3. Average hourly ED activity of purple martins for three days in each of the stages of the breeding cycle from laying to post-breeding, nest-cavity defence. 9
- Figure 4. A comparison of mean morning ED activity for two pairs of purple martins for which the stages of the breeding cycle coincided 13
- Figure 5. Mean morning ED activity curve for purple martins with three young. 15
- Figure 6. Wind velocity plotted against purple martin ED activity during the nestling stage. 33
- Figure 7. A comparison of the laying and hatching dates between female martins mated to males in adult plumage and those in yearling plumage in the same colony, Edmonton area, Alberta 63
- Figure 8. Laying and hatching frequencies for purple martins in the Edmonton area, Alberta 67
- Figure 9. A growth curve of wing lengths in purple martin nestlings based on two nests each containing three nestlings in 1965 at Edmonton, Alberta. 74
- Figure 10. A growth curve of wing lengths in purple martin nestlings based on three nests each containing five nestlings in 1965, at Edmonton, Alberta. 75

Figure 11. Mean morning activity on a per hour basis for each day during the nestling stage for nests containing one to seven young. 80

I N T R O D U C T I O N

Purple martins (Progne subis), North America's largest swallow, nest from southern Canada to northern Mexico and winter in South America (Peterson, 1961). In primeval times their distribution within this range, during the breeding season, was presumably dependent upon the presence of available abandoned cavities in forest trees which served as nest sites. Today, however, they nest almost exclusively in artificially constructed nest boxes.

Early Alberta naturalists reported martins nesting in small colonies in burned-over forests of central Alberta (K. Wood, pers. comm.). My observations taken from central Alberta northward to the arctic coast indicate that Edmonton, which has about 2000 nesting pairs, is near the northern limit of their breeding range. Scattered pairs are found north of this city for about 150 miles. The available nest boxes and abandoned cavities, created mainly by woodpeckers, which occur along the Mackenzie River to the Arctic are not used by purple martins.

Purple martins are one of several species of birds which depend almost exclusively on aerial invertebrate life for food, (Allen and Nice, 1952). Numerous authors have recorded the influence of weather upon the numbers of insects present in the atmosphere (Hardy and Milne, 1938; McClure, 1938; Glick, 1939, 1942, 1955; Freeman, 1945;

Ayre, 1958; Glick and Noble, 1961; Williams, 1961).

Survival of purple martins therefore seems linked indirectly with weather conditions. Forbush (1904) has stated that several days of rain, following a drought, eliminated martins from most of Massachusetts and other New England states. Losses of these birds are reported at other localities under similar conditions (Jones, 1917; McConnell, 1918; Bent, 1942; Allen and Nice, 1952). Apparently many days of cold and/or rain reduced aerial insects to such an extent that martins died of starvation. One object of this study was to determine the influence of weather conditions on the general activity of purple martins.

Changes in climate occur with changes in latitude. This is reflected in the biology of species with wide latitudinal ranges. Lack (1947) has stated that productivity as a function of clutch size increased from the tropics towards the poles for individual species nesting over a wide latitude. Since Allen and Nice (1952) have documented the breeding biology of purple martins in Michigan, it was appropriate to compare their findings with the situation at Edmonton. A second objective of this study was to determine the characteristics of the breeding biology of this species at the northern limits of its breeding range.

P R O C E D U R E

In order to determine the impact of weather conditions on purple martins, I decided to choose one phase of their activity for measurement. I had noted previously that martins spend a great deal of time passing in and out of the nest boxes. I decided to record this specific activity pattern as representing overall activity.

The entrances and departures from the nest box (hence forward referred to as ED activity), were recorded in 1965 from a colony of eight nesting pairs of purple martins at the A. Porcher residence in east Edmonton (Appendix I). In 1966, this activity was recorded at 18 nests near park headquarters at Elk Island National Park, 25 miles east of Edmonton (Appendix II).

The ED activity of the birds was recorded from photo-electric sensing devices mounted at the nest entrance (Appendix III). When a bird passed through the light beam on entering or leaving the nest, the impulse was recorded on an Esterline Angus recorder. Several electronic difficulties arose in 1965 through using an inappropriate light source and wiring. These were corrected in 1966 and little trouble was experienced. Details of the wiring diagrams may be examined in Appendix IV.

Purple martin ED activity was recorded continually from May 28 through August 17, 1965 and from May 23 through August 30, 1966. A typical record is shown in

Figure 1. It is evident from this figure that martins did not always move completely through the entrance but remained resting therein for varying lengths of time. When compiling the data I arbitrarily decided that if the bird had blocked the light source for less than one minute, only one pass was recorded. However if the bird blocked the light source for longer than one minute, then two passes were noted, one for entering the small photo-electric box and one for departing. For example, during the half-hour interval shown in Figure 1, channel 5 would register 5 EDs, channel 12 - 7 EDs and channel 13 - 9 EDs.

Several of the nest boxes faced west into the afternoon sun. When sunlight shone directly into the next entrance, a bird passing through failed to activate the light sensitive resistor, thus much of the afternoon activity was lost. Because of the interference of sunlight I decided, for all nests, to utilize only morning activity which is represented by the time from beginning of morning civil twilight until 1230 hours.

Civil twilight commences when the sun is 6° below the horizon and ends when it reaches the horizon (List, 1951). This time at Edmonton varies from 42 minutes on May 1, to 55 on June 21, and back to 25 minutes on August 25 (List, op.cit.).

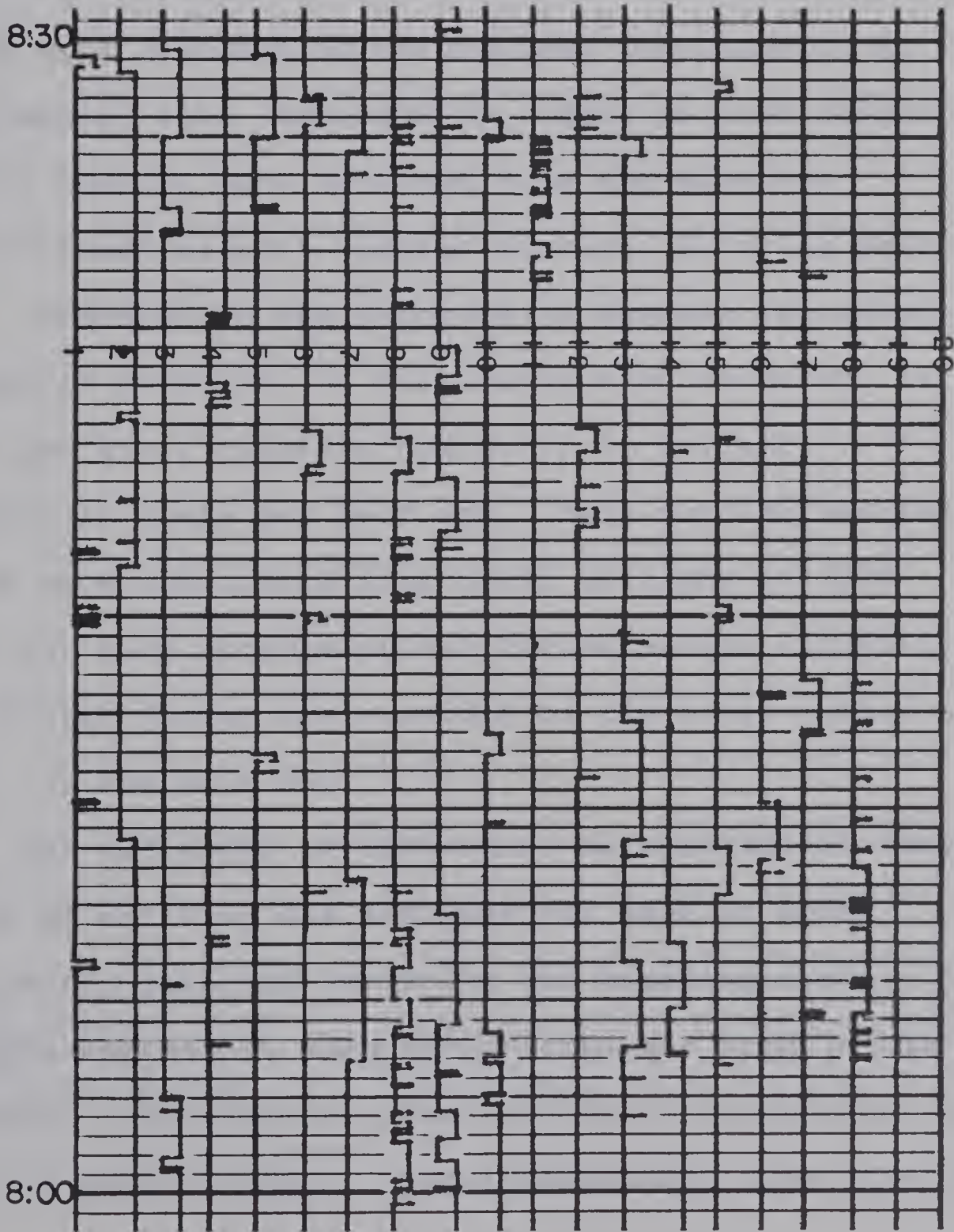
Figure 1. Record of purple martin ED activity taken from a 20-channel Esterline Angus recorder. This record was taken on June 24, 1966 from 0800 to 0830 hours. Meteorological conditions were as follows:

Temperature, 58°F;
Wind velocity, calm;
Sky opacity, 9;
Relative humidity, 59%;
Barometric pressure, 31.5 m.b.

Activity represented was by pairs of birds at different stages in the breeding cycle as noted along the side of the Figure.

Channel Stage in breeding cycle

- 1-Feeding 7 young, 4 days old
- 2-Incubation
- 3-Nesting
- 4-Incubation
- 5-Incubation
- 6-Poor photo-cell: not used
- 7-Incubation
- 8-Nest defence
- 9-Visitor, not used
- 10-Incubation
- 11-Nest defence
- 12-Incubation
- 13-Incubation
- 14-Nest defence
- 15-Incubation
- 16-Egg laying
- 17-Incubation
- 18-Visitor, not used
- 19-Not connected
- 20-Not connected



The data were summarized by obtaining the mean morning activity for each nest. This mean value will henceforth be the ED activity discussed.

Most meteorological data were obtained in 1965 from the Department of Transport Weather Station 3.75 miles northwest of the experimental site. In 1966, temperature, relative humidity and barometric pressure and hours of rainfall were recorded 30 inches above ground with standard meteorological instruments, at the experimental site (Appendix V). Data on wind velocity and sky opacity were obtained from the Edmonton International Airport Weather Station, 41 miles southwest. Temperature was recorded in degrees Fahrenheit; barometric pressure, in millibars; wind velocity, in miles per hour; relative humidity, in percent; rainfall in hours per half day. Mean morning weather values were calculated from civil twilight to 1200 hours for each meteorological factor except rainfall. This latter factor was recorded as the total number of hours for the half day.

The influence of individual meteorological factors on the ED activity was analysed for each of seven arbitrarily-selected stages in the breeding cycle. A multiple regression computer program was used in the analysis. Correlations were considered significant at the five percent level. Significance was determined by

comparison of the correlation factors with confidence-belt graphs from Bennett and Franklin (1954). The impact of several weather factors acting together upon the ED activity was studied using a graphical form designed by Hardy and Milne (1938) but expanded to include up to four weather factors.

To facilitate comparison of weather factors with activity at the nest entrance, the breeding cycle was divided into seven stages. They are as follows: arrival, nest-cavity defence and pair-bond formation; nest building; nest completion; laying; incubation; nestling; and post-breeding defence of nest cavity. Typical examples of ED activity within each of these stages are illustrated in Figures 2 and 3.

Breeding biology data for each of the seven stages were recorded at all nests under study. In 1965, the eight electronically wired nest boxes were occupied for all or part of the season and will be called henceforth the "experimental nests". Thirteen unequipped nests were occupied for all or part of the season and will henceforth be called the "control nests". The latter were located from 30 feet to 7.5 miles from the experimental nests. At Elk Island in 1966, the 18 electronically equipped nests were the experimentals. Controls were 14 unequipped nests at the same site and four others

Figure 2. Average hourly ED activity of purple martins for three days in each of the stages of the breeding cycle from arrival to nest completion. These data were collected in 1966 at Elk Island National Park. Birds involved include from top to bottom:

- A. Yearling male; female arrived June 8.
- B. Yearling male arrived June 20; female arrived June 23; nest building began June 24.
- C. Adult male; nest building began May 25 or 26; nest completed May 30.
- D. Same pair as "C"; nest building complete May 30; first egg laid June 12.

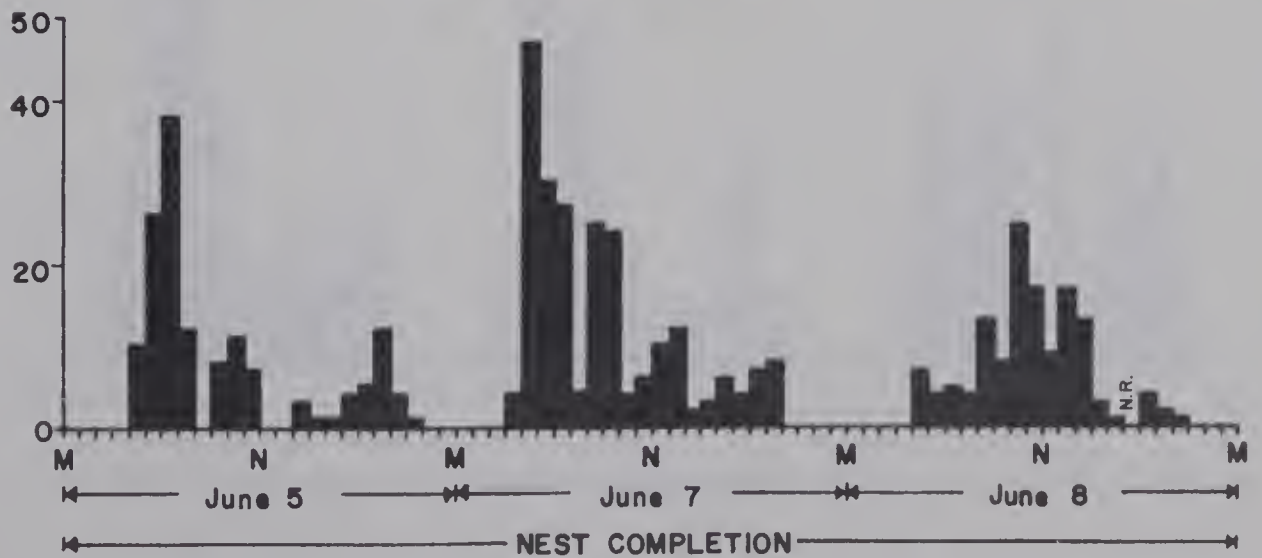
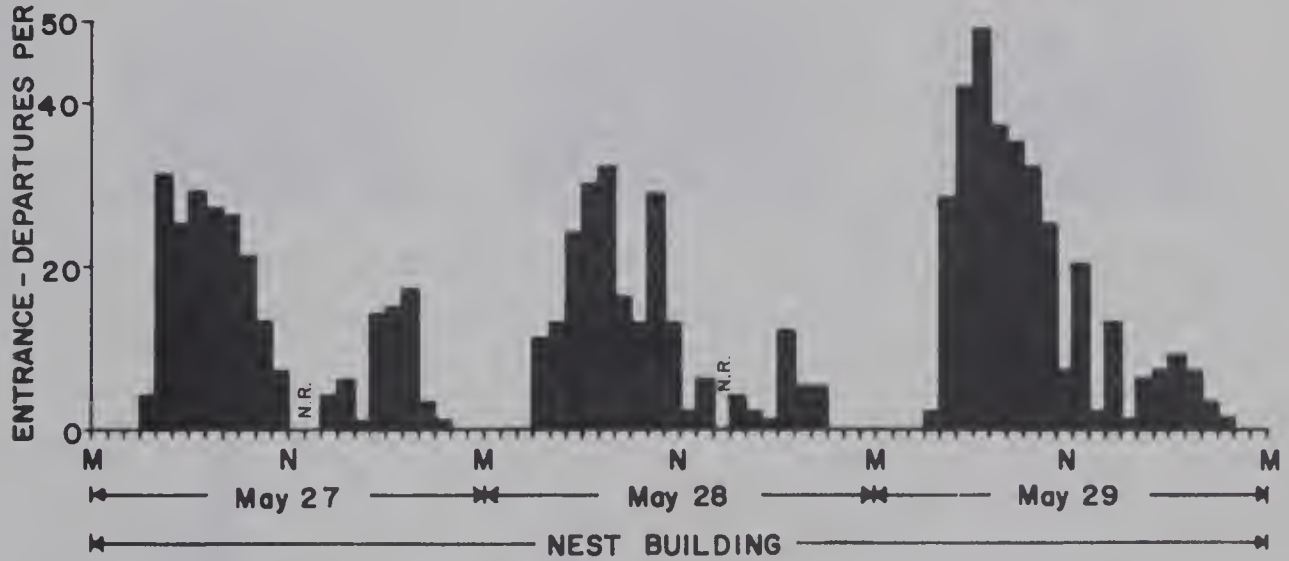
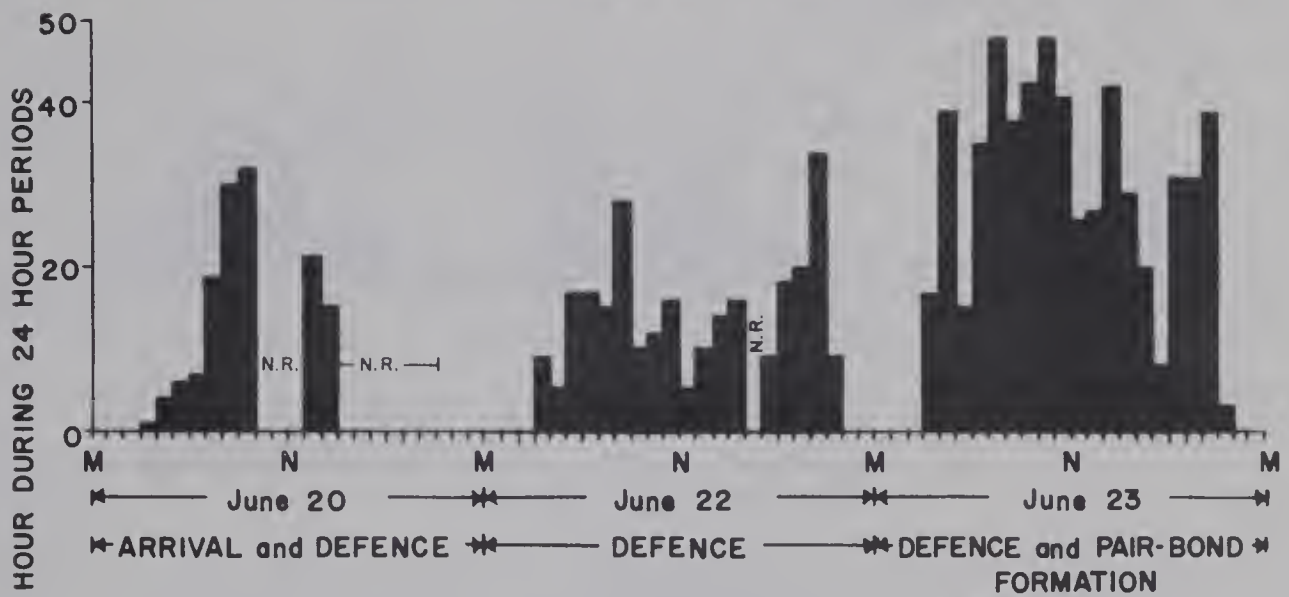
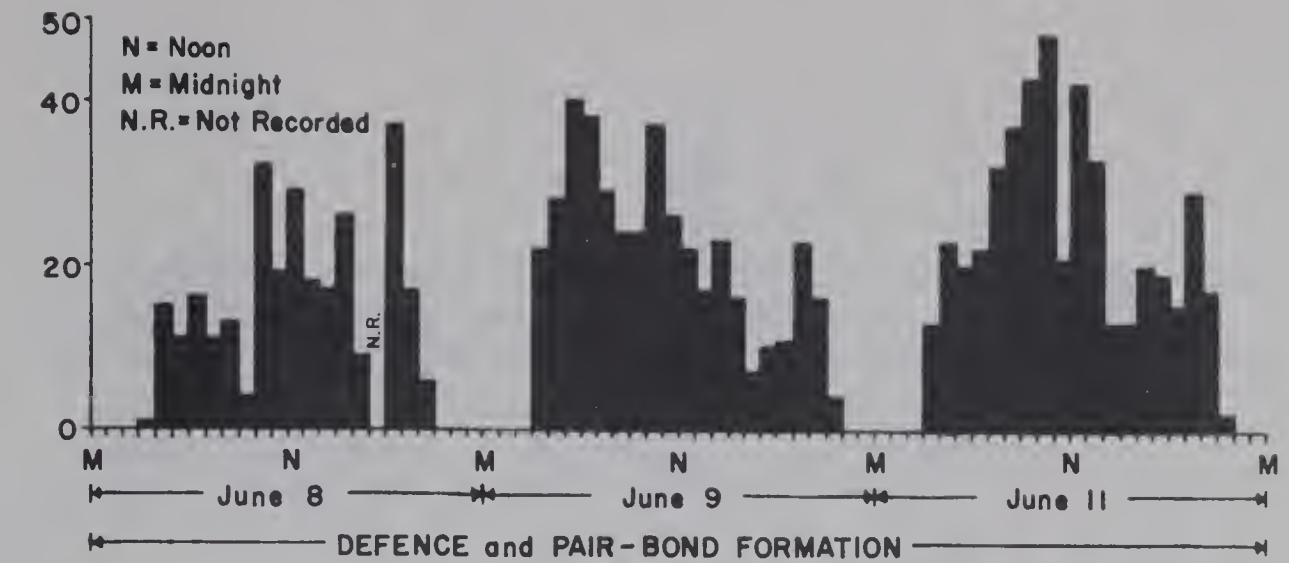
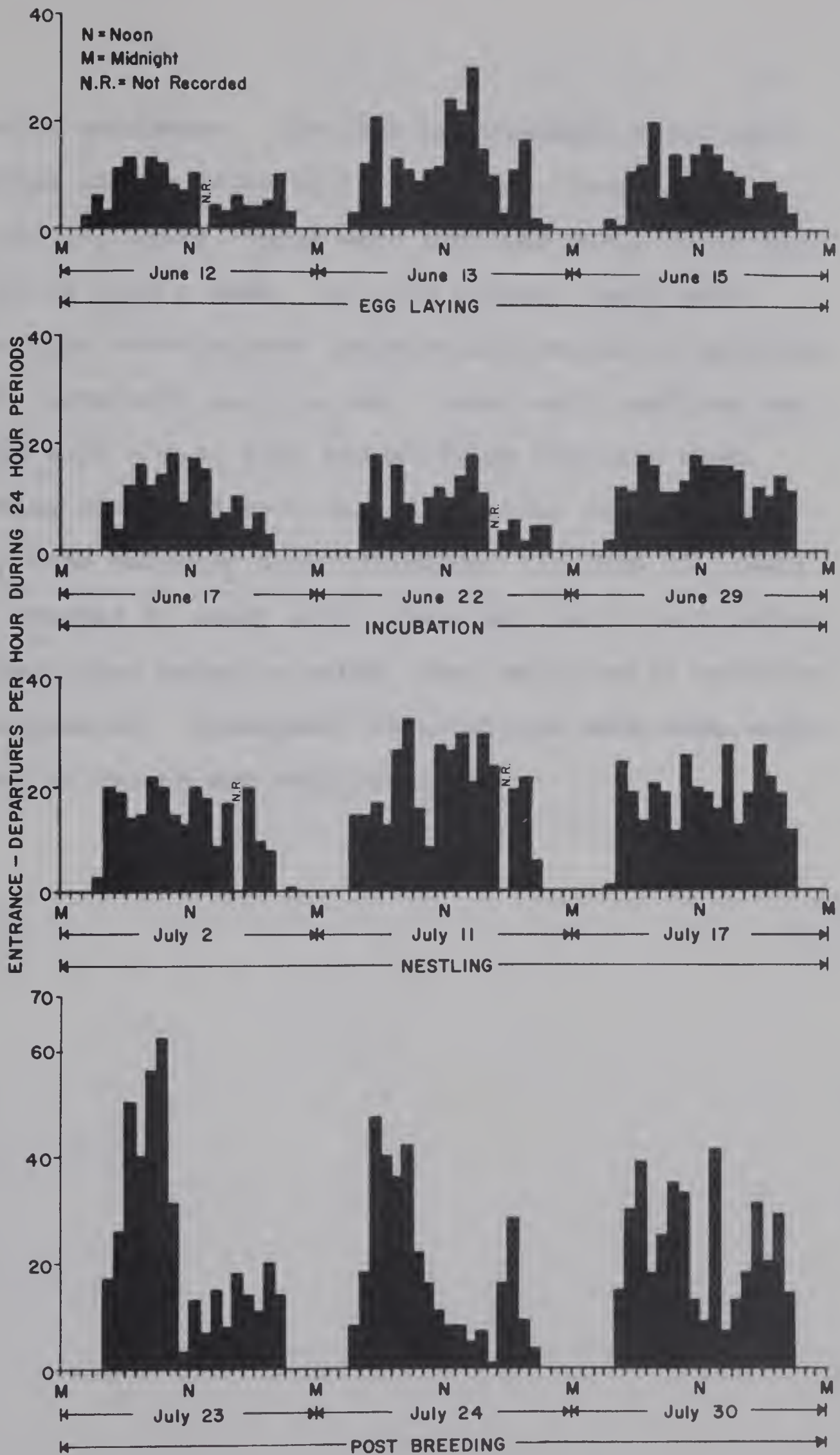


Figure 3. Average hourly ED activity of purple martins for three days in each of the stages of the breeding cycle from laying to post-breeding nest-cavity defence. These data were collected in 1966 at Elk Island National Park. Birds involved include from top to bottom:

- A. Same pair as in Figure 2 "C" and "D"; first of five eggs laid June 12; last egg laid June 16.
- B. Same pair as "A" above; incubation began June 16; first young hatched July 1.
- C. Same pair as "A" and "B" above; 3 nestlings, two hatched July 1, the third July 2.
- D. Yearling male began defending cavity July 23; female joined in defence July 27; adult male alone defending cavity July 30.



22 miles southwest. The 1965 experimental nests were examined almost daily until all young fledged. Of the control nests, three were examined every third day, and three once a week. At five control nests each young upon hatching was individually marked by painting their claws with nail polish. Later each nestling was banded with a U.S. Fish and Wildlife aluminum band. The wing chords of each marked nestling were measured daily from hatching until fledging. In 1966 all nests were checked at least every other day until just before the nestlings began to hatch, then daily until hatching was completed. Subsequent observations were made every second to fourth day until fledged.

RESULTS AND DISCUSSION

INFLUENCE OF WEATHER

The suitability of mechanical recording equipment, when used to study animal activity is often questioned. Table 1 presents the results of three different, 3-hour observation periods spent comparing the recorded ED activity with the observed. These observation periods were undertaken to determine the percentage of error in the recording equipment. It is apparent that 99 percent of the ED activity observed was mechanically recorded. I assume this high percentage of accuracy occurred throughout the entire recording period.

Table 1. A comparison of purple martin ED activity recorded mechanically and observationally over 3-hour periods in 1966

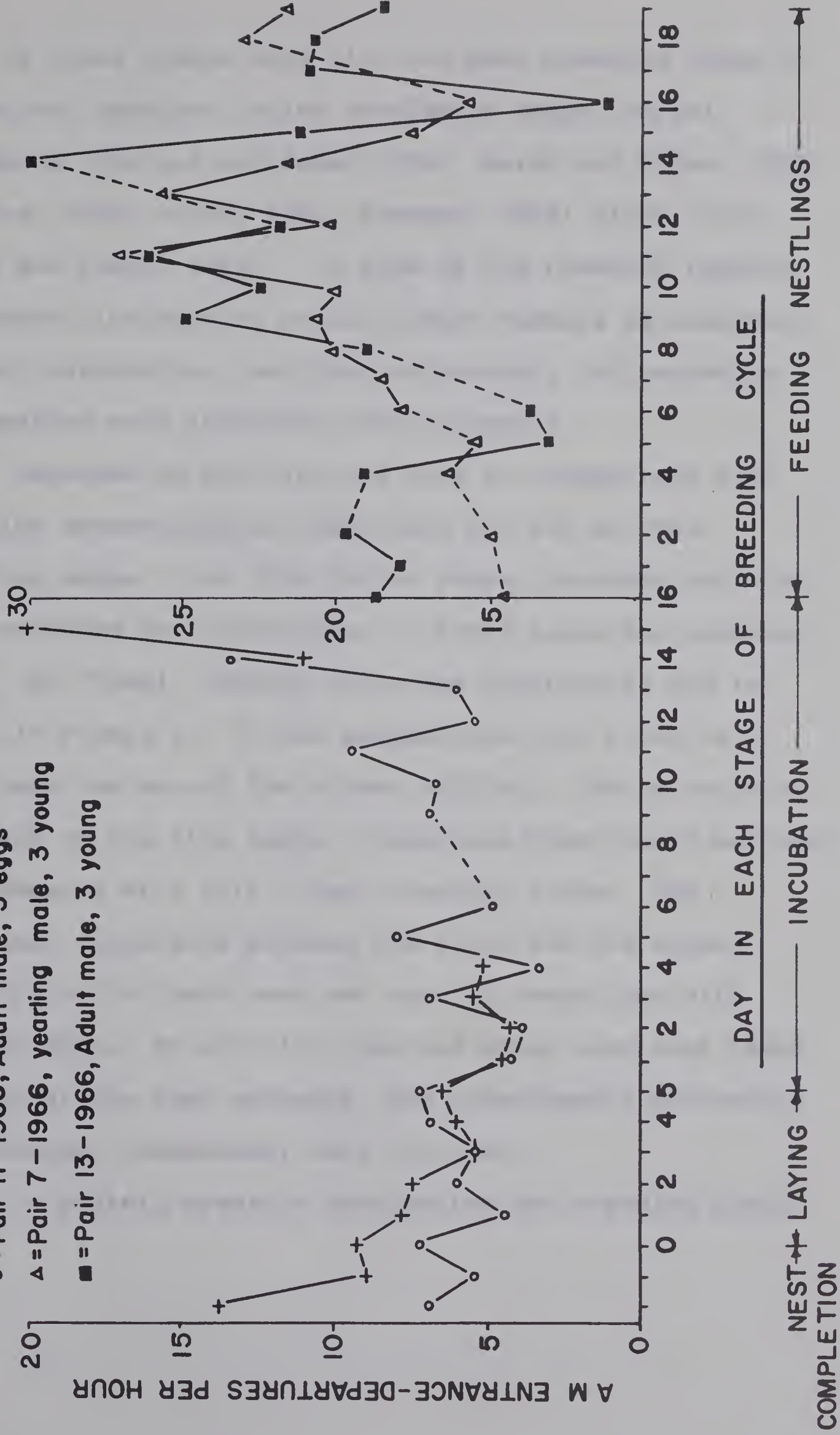
Method of recording	Date and time of recordings			Total	Percent efficiency
	July 13	July 20	July 27		
	0445-0747 hrs	0430-0730 hrs	0430-0730 hrs		
Observed and mechanically recorded	377	429	441	1247	99
Observed but not mechanically recorded	7	2	3	12	

It was assumed that purple martins at the same stage in the breeding cycle and with the same number of nestlings, would react similarly to specific meteorological conditions in terms of activity at the nest entrance. To test this assumption the activity data from two nests were compared (Fig.4). The figure illustrates activity of four pairs of martins, two of which express ED activity from nest completion through incubation, the other two pairs through the nestling stage. The number of eggs, nestlings and weather were identical for each set of two pairs. Using the "Wilcoxon Two-Sample Test for the Unpaired Case" given in Alder & Roessler (1964), there was no significant difference in activity between members of pairs during the laying, incubation and nestling stages. I assumed that activity in the other stages would be similarly comparable.

Purple martins feed almost exclusively on aerial insects. These are caught while flying between 100 and 200 feet above ground, (Beal,1918; Johnston,1967), however food may be taken from a few feet to over 500 feet, (Allen and Nice, 1952; Johnston and Hardy,1962). The six orders of insects found most abundant in purple martin gastro-intestinal tracts were Hymenoptera, Diptera, Hemiptera, Coleoptera, Lepidoptera and Odonata (Beal,1918; Johnston 1967 and pers. comm.). The first

Figure 4. A comparison of mean morning ED activity for two pairs of purple martins for which the stages of the breeding cycle coincided

+ = Pair 7-1965, yearling male, 5 eggs
 o = Pair 11-1965, Adult male, 5 eggs
 Δ = Pair 7-1966, yearling male, 3 young
 ■ = Pair 13-1966, Adult male, 3 young

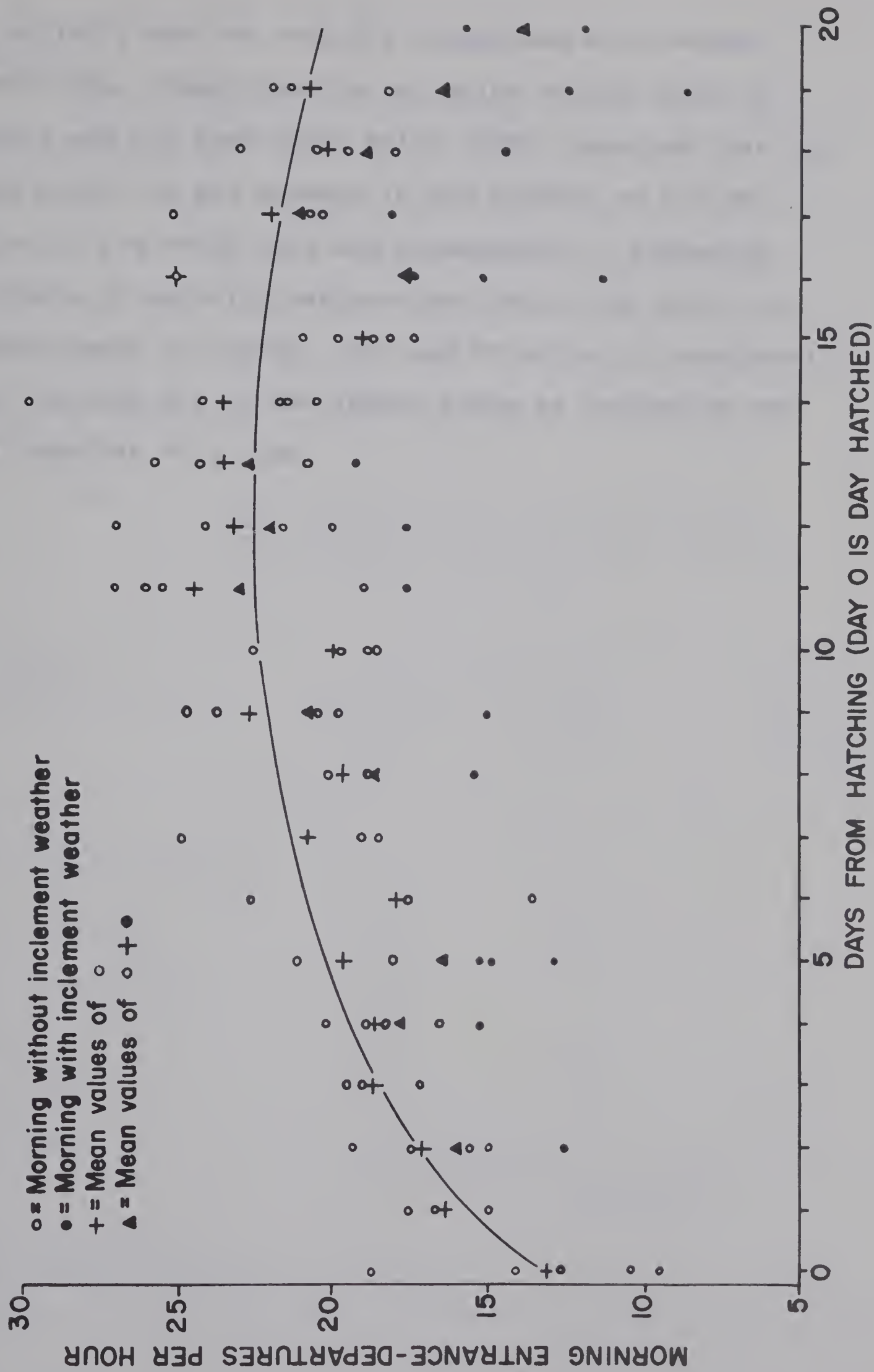


four of these orders were also the most numerous taken by mechanical samplers during studies of insect aerial abundance (Collins and Baker, 1934; Hardy and Milne, 1938; McClure, 1938; Glick, 1939; Freeman, 1945; Glick, 1957; Glick and Noble, 1961). In view of the numerous reports of weather influencing aerial insect numbers as reported in the introduction, martins are probably influenced by the weather more indirectly than directly.

Recorded ED activity was used for comparison with changing meteorological conditions for all but the nestling stage. For this latter stage, recorded activity was corrected for differences in brood sizes and nestling ages. An "ideal" feeding curve was constructed and is shown in Figure 5. It was assumed that all young in a nest were the age of the oldest sibling. The ED activity for each of the five nests, containing three young per nest, was compared with this "ideal" feeding curve. The numerical difference between the curve and the actual ED activity for each nest was used in comparison with weather data. ED activity recorded after nestlings began begging at the nest entrance, and consequently activating the recorder themselves, were not used.

On certain specific days during the breeding cycle

Figure 5. Mean morning ED activity curve for purple martins with three young. Curve was drawn by inspection ignoring ED activity on cold, rainy or windy days.



ED activity was not used for comparison with weather conditions. Data from the day prior to the onset of laying was not used since Welty (1962) reported that in some birds the egg appears in the oviduct on the day prior to its being laid and consequently I suspected a change in activity patterns may occur just prior to commencement of laying. Nor was ED activity considered for the last day of the laying stage as incubation was initiated at this time.

Rainfall

Casual observations of martins during rain indicated they remained near the colony, resting on adjacent trees and wires. Table 2 demonstrates that activity was influenced by periods of rainfall. ED activity during the nest building, nest completion, incubation and nestling stages was reduced by one half or more during rain. Activity also was reduced somewhat during the arrival and post-breeding stages.

Table 2. Comparison of mean ED activity with that recorded while rain fell during the different stages of the breeding cycle of purple martins

Stage in breeding cycle	Mean ED activity		Sample size during rainfall
	Throughout stage	During rainfall	
Arrival, nest-cavity defence pair-bond formation	13.6	11.4	29
Nest building	19.4	10.6	40
Nest completion	14.9	7.8	7
Laying	10.9	14.2	2
Incubation	9.3	4.4	10
Nestling	0 (departure from "ideal") -6.8 (refer opposite)		10
Post-breeding nest-cavity defence	11.2	8.0	12

Purple martins feed on aerial arthropods as mentioned earlier. Literature reports indicate aerial insect abundance decreases during rainfall (McClure, 1938; Freeman, 1945; Lewis, 1950; Minar, 1962). I assumed that this decrease would mean purple martins would spend greater amounts of time searching for food and hence a decrease in ED activity would result.

The ED activity during the laying stage appeared to increase during rainfall (Table 2). I have no explanation for this increase except that there was very little data - one pair on two separate rainy days.

Purple martins will return to nest boxes for shelter during prolonged periods of rain, even after all young have fledged. On August 11, 1966 rain fell over a period of 8 hours during the day. That evening color-banded martins, which had not been seen for 3 days, re-appeared, entered the nest cavities and remained there for the night. The rain had ceased by the following morning and the martins were not seen at the nest boxes again that season.

The reduction of activity by rainfall as noted above, is similar to that reported by several authors. Moreau (1939) noted that during heavy rain there was a decrease in numbers of nestling feedings by wire-tailed swallows (Hirundo s. smithii). Purchon (1948)

showed that European swallow nestlings (Hirundo rustica) starved in rainy weather. Koskimies (1950) and Lack and Lack (1951) showed a negative correlation between duration of rain and the number of trips made by adults to feed nestlings. Similarly Otto in Allen and Nice (1952) noted the rate at which purple martins were feeding nestlings dropped from well over 200 feedings per hour to between 119 and 132 per hour during light rain. When rain ceased the following hour, trips increased to 459 per hour.

An examination of the ED activity data indicated that if the rain interval lasted 3 or more hours, the mean morning ED activity value was substantially reduced. In view of this significant influence, I discarded activity measured on mornings with 3 or more hours of rainfall when considering the other weather factor comparisons with activity.

Temperature

The influence of the temperature near the ground upon the abundance of aerial arthropods, which form the major food of purple martins, is well documented in the literature (Pinchin and Anderson, 1936; Hardy and Milne, 1938; McClure, 1938; Glick, 1939, 1957; Freeman, 1945; Wellington, 1945; Lewis, 1950; Glick and Noble, 1961; Williams, 1961; Cloudsley - Thompson, 1962; Minar, 1962). Since purple martins feed on these forms, the birds' activity should indirectly be influenced by temperature.

Temperatures taken in this study were measured near the ground. According to A. Mann (pers. comm.) the near ground temperature may be as much as 5°F lower than at 500 feet, on a clear, calm morning. The difference is reduced if there is any wind.

Because ED activity was averaged over the half-day, mean temperatures were similarly computed. The mean ED activity and mean temperature were then compared, as shown in Table 3, throughout the breeding cycle.

Table 3. The relationship between purple martin activity at the nest entrance and temperature during the major divisions of the breeding cycle

Stage of breeding cycle	Correlation coefficient	Sample size	Level of significance		Equation of line
			5%	1%	
Arrival, pair-bond formation	0.04802	22	0	0	
Nest building	0.21113	24	0	0	
Nest completion	0.70797	16	+	+	$y = 11.57 + 0.539x$
Laying	0.56751	19	+	0	$y = 3.95 + 0.126x$
Incubation	0.16734	23	0	0	
Nestling	0.50800	14	0	0	
Post-breeding	-0.71014	20	-	-	$y = 34.17 - 0.385x$

Significant correlations were demonstrated between ED activity and temperature during the nest completion, laying and post-breeding stages. I suggest that the significant correlation shown at the one percent level for activity during the nest completion stage may indicate that during warm weather martins gathered sufficient food in a short time, and then were free to defend the nest cavity, which resulted in increased ED activity. In cooler weather birds would spend more time gathering food and ED activity associated with nest defence would decrease. Similar conditions

would explain the significant correlation at the five percent level during the laying stage.

The post-breeding stage showed a negative correlation with temperature. During this post-breeding stage, martins may be influenced by two opposing physiological drives: 1) hyperphagia in association with Zugruhe, and 2) territoriality in response to fall recrudescence of the gonads. During warm weather martins may respond to the drive to feed and thus desert the colony, whereas, during cooler weather, when food is less plentiful the birds may spend a maximum amount of time defending future nest sites. Table 4 illustrates the reduction of ED activity as the mean temperature rose. There was about a one-third decrease in ED activity above 59°F.

Table 4. Influence of temperature upon ED activity in the post-breeding nest-cavity defence stage of the purple martin breeding cycle

Temp. °F.	Mean ED activity	Sample size
50-54	13.5	18
55-59	14.3	25
60-64	9.4	27
65-69	8.0	18
70-75	5.9	4
Mean throughout stage	11.2	

The arrival, nest defence, pair-bond formation stage did not show a significant correlation with temperature. However on the one day with a very low mean temperature of 37°F, the mean ED activity was 7.8, well below the overall mean of 13.8 for this stage (Table 5.)

Table 5. Influence of temperature upon ED activity in the arrival, nest defence, pair-bond formation stage of the purple martin breeding cycle

	Temp. °F	Mean ED activity	Sample size
1966	35-39	7.8	7
	40-45	14.4	26
	46-50	17.1	25
	51-55	14.1	37
	56-60	11.4	19
	61-65	11.8	8
	66-70	16.4	9
Mean throughout stage		13.6	

The ED activity during the nestling stage did not show a significant correlation with temperature (Table 3.) However during the 4 days on which the temperature fell below 55°F, ED activity was below normal. On July 21, 1966, the mean temperature was 50°F, and the activity was 9.6 points below a calculated normal. I postulate that if additional activity data were collected at these lower temperatures, a correlation could be demonstrated. During this stage adults attempt to carry a certain amount of food to the brood. If food is abundant, demands of the nestlings will be met. If not, then trips to the nest will decrease.

These results compare favourably with those

reported in the literature. Jacobs (1903) stated several martins will crowd into one nest during cold weather, presumably to conserve heat. Koskimies (1950) showed that the time of departure from the nest in the morning by European swifts (Apus apus) is dependent on temperature. Paynter (1954) reported that cold days inhibited the nest building of tree swallows (Iridoprocne bicolor).

Since there appears to be some indirect influence by temperature upon martin ED activity, I wondered if there would be a correlation between monthly mean temperatures and different stages in the breeding cycle at the northern limits of the breeding range. Table 6 illustrates the temperature means for the Edmonton area. The May temperatures are below the 55°F threshold value at which the aerial abundance of insects is significantly decreased (Glick, 1939). These May temperatures are also near the lower end of a "zone of transition" between 50°F and 58°F below which insect activity decreased (Wellington, 1945). In June the temperatures in Table 6 are above the 55°F threshold and within the upper limits of the "zone of transition". Enough food is probably available in the latter month to allow martins to participate in nest building, laying and incubation. Later, during July, the mean

Table 6. Mean temperatures over many years at Edmonton and in the rural surroundings for the months of May to August inclusive

Month	Temperature	
	Edmonton	Rural
May	52.1°F	50.9°F
June	57.8°F	56.4°F
July	63.1°F	61.6°F
August	60°F	58.6°F

temperatures are at levels sufficiently high to assure that aerial insects will be abundant. Martins hatch in July and presumably encounter the greatest number of aerial insects at this time. Therefore, insect abundance probably does not limit this bird at the northern edge of its breeding range.

Sky Opacity

Sky opacity as used in this study is a measure of the available light. It is the amount of the celestial dome which is covered by cloud through which blue sky is not visible. A high numerical sky opacity value means an overcast sky, whereas a low numerical value is registered on a clear day. The use of cloud cover, usually considered in other animal studies, does not take into account the amount of actual sunlight penetrating through clouds, particularly if the clouds are of the cirrus variety.

Sky opacity values were taken periodically at Elk Island National Park in 1966 and compared with those readings from the International Airport. Conditions were almost identical except when a weather front was passing. At this time cloud cover changed about an hour earlier at the airport since weather systems generally move from west to east in this area.

Insects are stimulated to increased activity as light intensity increases up to a certain level of intensity as reported by a number of workers (McClure, 1938; Hardy and Milne, 1938; Glick, 1939; Barr et al, 1960; Minar, 1962; Maslov, 1964). Taylor, (1963) claimed that once an optimum level of light intensity was reached, temperature became the primary factor

influencing insect activity.

I presume purple martins hunt more efficiently in bright sunlight than in complete overcast since insects would be more abundant and possibly more visible to the bird.

In this study sky opacity was compared with ED activity. Table 7 illustrates the coefficients and levels of significance. Significant negative correlation coefficients were found for the incubation and nestling stages.

Table 7. The relationship between purple martin activity at the nest entrance and sky opacity during the major divisions of the breeding cycle

Stage of breeding cycle	Correlation coefficient	Sample size	Level of significance		Equation of line
			5%	1%	
Arrival, pair-bond formation	-0.19055	28	0	0	
Nest building	0.11299	33	0	0	
Nest completion	-0.31946	19	0	0	
Egg laying	-0.36779	30	0	0	
Incubation	-0.52443	39	-	-	$y = 12.23 - 0.431 x$
Nestling	-0.47524	19	-	0	$y = 1.87 - 0.589 x$
Post-breeding	0.22799	27	0	0	

During incubation, on bright, clear days I postulate that males can feed efficiently and hence have more time to defend the nest, resulting in an increased ED activity. During dull days there is less food and visibility is reduced, hence less nest defence activity.

On clear to partly cloudy days ED activity increased during the nestling stage. As mentioned above there would be more aerial insects during these clear days and consequently adults would locate food more easily, feeding nestlings oftener. The opposite would occur on overcast days. In addition dull days are usually cooler and hence females may possibly spend more time brooding young, reducing ED activity.

Light intensity appeared not to have as great an influence upon ED activity in the other five stages. However during the post-breeding stage, on dull days there was a substantial increase in activity, but insufficient data to produce a possible correlation. The increase of ED activity on dull days may be explained by the same reasoning as given for an increase of activity during this stage as the temperature fell; that is, sunny days stimulate martins to feed, and overcast skies stimulate them to defend future nest sites.

The significant correlations of ED activity with sky opacity are possibly co-incidental, since rain and/

or low temperatures usually occur on very dull days.

Results obtained from this study compare favourably to published reports. In Swifts (Apus apus) feeding activity increases on clear days and decreases on dull days (Lack and Lack, 1951).

The Esterline Angus records showed that purple martins left the nest in the morning during the period of civil twilight. On clear days they departed earlier than on dull days. This agrees with reports of other workers who state that the commencement of morning bird activity is positively related to light intensity (Elliot, 1932; Williams, 1941; Nice, 1943; Nice and Thomas, 1948; Palmgren, 1949; Brauner, 1952; Scheer, 1952; Armstrong, 1955; Groebbels, 1956; Weise, 1956; Leopold and Eyon, 1961; Davis, 1963; Schoennagel, 1963).

Wind Velocity

Wind velocities are important in aerial insect abundance. Insect aerial numbers are decreased during periods when wind velocity exceeds 6 mph, and particularly above 10 mph (Lewis, 1950; Glick, 1955, 1957; Williams, 1961; Cloudsley-Thompson, 1962). The greatest number of insects were collected by mechanical samplers in the atmosphere, during days in which wind speeds were between 5 and 6 mph (Glick, 1939, 1942; Freeman, 1945).

In this study wind velocity was compared with ED activity. Table 8 illustrates the coefficients of correlation and levels of significance obtained. Significant correlations were found during the nest completion and nestling stages. I presume that during these two stages high wind velocities increase the hunting time needed by martins to obtain food. During the nest-completion stage the amount of available time to defend the nest would be reduced, thus reducing the ED activity. Similarly, during the nestling stage, the number of feeding trips to the nest would decrease in high winds, reducing the ED activity.

Table 8. The relationship between purple martin activity at the nest entrance and wind velocity during the major divisions of the breeding cycle

Stage of breeding cycle	Correlation coefficient	Sample size	Level of significance		Equation of line
			5%	1%	
Arrival, pair-bond formation	0.17091	13	0	0	
Nest building	0.17056	15	0	0	
Nest completion	-0.58854	12	-	0	$y = 19.97 - 0.569x$
Laying	0.31648	14	0	0	
Incubation	-0.44743	15	0	0	
Nestling	-0.63362	12	-	0	$y = 1.92 - 0.487x$
Post-breeding	-0.42491	12	0	0	

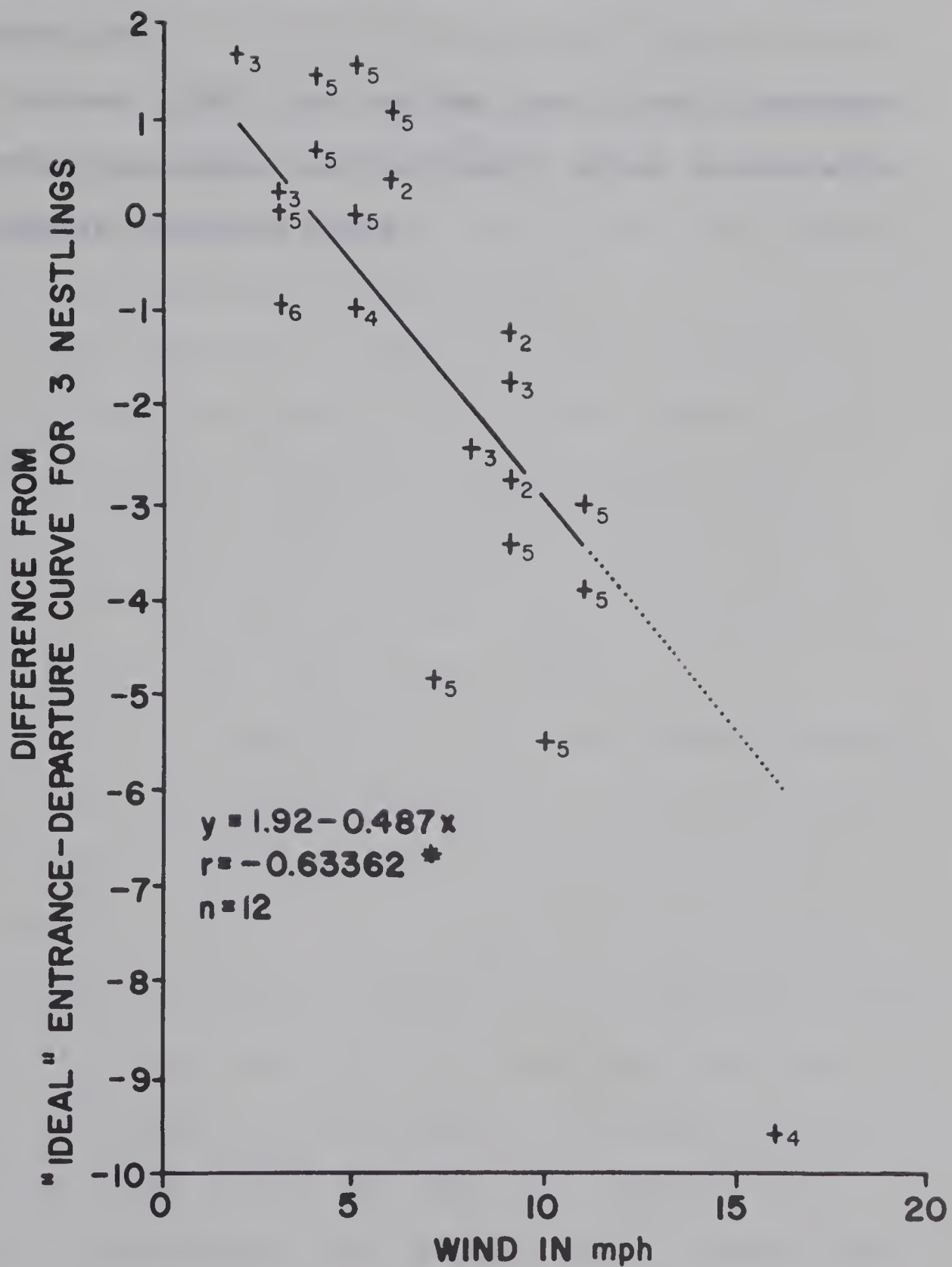
Figure 6 illustrates the rapid decrease in activity as wind velocity increases during the nestling stage. It is apparent that wind velocities below 6 mph do not appear to influence activity. As wind velocities increased to 10 mph activity values rapidly decreased. The one high wind velocity, 16 mph, substantially decreased activity. These results compare favourably with those reported by Lack and Lack (1951) in their study of swifts.

Activity during the incubation stage was not significantly influenced by wind. However the few days

Figure 6. Wind velocity plotted against purple martin ED activity during the nestling stage.

The points "+" represent departure values of activity from the "ideal" feeding curve under different wind velocities.

The numbers 2, 3, 4, 5, 6 represent the number of pairs at a particular wind velocity on a particular day.



in which wind velocities exceeded 13 mph there was a noticeably decrease in activity, suggesting that if more data were available a correlation might be demonstrated.

Scheer (1952) and van der Baan (1954) reported that wind decreases bird activity, which agrees with the results reported above.

Relative Humidity

Very little information is available on the influence of humidity upon the activity of aerial insects. Lewis (1950) has summarized the literature. Glick (1939, 1942, 1955) found the number of insects in the upper air to show no relationship to relative humidity, whereas Hardy and Milne (1938) and Freeman (1945) indicated some correlation.

Little mention is made of relative humidity in the ornithological literature. A few workers noted a weak positive or negative correlation between relative humidity and bird activity (Elliot, 1932; Palmgren, 1935; Armstrong, 1955; Leopold and Eyon, 1961; Prince et al, 1965; and Verner, 1965).

Data were analyzed for the relationship between ED activity and relative humidity. The correlation coefficients and their level of significance are presented in Table 9. It is apparent that the only significant correlation was during the nestling stage and that it was negative. It was noted that high relative humidity values usually occurred on overcast days which often had some rain, whereas low humidity occurred on fair weather days. During the nestling stage the adults must feed both themselves and their young. Consequently, days with high relative humidity which usually reflected weather con-

ditions when insect numbers were reduced, tended to result in decreased ED activity.

Table 9. The relationship between purple martin activity at the nest entrance and relative humidity during the major divisions of the breeding cycle

Stage of breeding cycle	Correlation coefficient	Sample size	Level of significance		Equation of line
			5%	1%	
Arrival, pair-bond formation	-0.12746	21	0	0	
Nest building	-0.24474	31	0	0	
Nest completion	-0.18922	21	0	0	
Laying	-0.23559	21	0	0	
Incubation	-0.21614	31	0	0	
Nestling	-0.59897	12	-	0	$y = 13.14 - 0.226x$
Post-breeding	-0.05533	19	0	0	

The mean relative humidity during the nestling stage ranged from 55 to 73 per cent. Hardy and Milne (1938) reported aerial insect numbers decreased as the humidity rose from 37 to 73 per cent. Freeman (1945) found a similar reduction in insect numbers between 65 and 73 percent. Relative humidity rises as temperature decreases (if the water content of the air remains constant).

The mornings with high relative humidity usually coincided with cool temperatures and consequently the relative humidity influence upon martins may only be coincidental and not causal.

Upon examining data throughout each of the other breeding cycle stages, it was found that incubation activity was the only one with any possible relationship to relative humidity. ED activity in this stage showed a negative correlation above 65% but none below this level. The temperature-relative humidity relationship may be showing up at these higher humidity values in this stage.

Barometric Pressure

Literature references on the influence of barometric pressure upon insect activity are not numerous. Entomologists generally agree that a change in barometric pressure affects insect activity particularly falling pressure which stimulates greater flight activity (Glick, 1939; 1942; Wellington, 1945; Lewis, 1950; Dethier, 1957; Edwards, 1961). Some of these authors noted a relationship between barometric pressure per se and insect activity (Glick, 1939; Lewis, 1950; Edwards, 1961), whereas other workers report no influence (Hardy and Milne, 1938).

Since pressure changes appeared to influence flying insects of several species, calculations were made to determine whether a relationship existed between pressure change and martin activity. A list of the calculated correlation coefficients is presented in Table 10. Additional analyses were made to determine whether correlation existed between activity and barometric pressure per se. No significant correlation between barometric pressure per se and ED activity during any of the stages in the breeding cycle was found. However, correlation coefficients were significant at the one per cent level between pressure change and ED activity in two breed-

Table 10. The relationship between purple martin activity at the nest entrance and rising and falling barometric pressure during the major divisions of the breeding cycle

Stage of breeding cycle	Falling Barometric Pressure			Rising Barometric Pressure		
	Correlation coefficient	Sample size	Level of significance 5% 1%	Correlation coefficient	Sample size	Level of significance 5% 1%
Arrival, pair-bond	-0.29434	6	0 0	0.25268	8	0 0
Nest building	0.13830	9	0 0	0.14460	11	0 0
Nest completion	0.72311	5	0 0	0.00365	8	0 0
Laying	-0.87375	7	- -	0.57970	10	0 0
			$y = 5.019 - 2.617x$			
Incubation	0.02206	13	0 0	-0.13006	11	0 0
Nestling	-0.08590	7	0 0	-0.99009	5	- -
						$y = 8.798 - 4.194x$
Post-breeding	-0.02167	10	0 0	-0.25781	8	0 0

ing cycle stages: laying and falling pressure; nestling and rising pressure.

In view of the reports in the literature that falling pressure results in an increased number of aerial insects, it was surprising that ED activity in only one stage - laying, showed a significant correlation. Professor Longley of the Department of Geography, University of Alberta, informed me that Edmonton's proximity to the mountains results in irregular weather systems. Typically, falling pressure should indicate cloud, wind and rain, all indirectly influencing martin activity. This situation does occur if the low pressure system develops with east winds to the south over Red Deer. However, if the system develops to the north around Lesser Slave Lake, accompanying west winds bring clear skies. I assume that since data were collected throughout the season, these opposing weather conditions would counteract each other with a resultant lack of correlation between falling pressure and ED activity. Correlation between laying activity and falling pressure may be explained by probable similar weather conditions existing on the seven days in which activity was measured when pressure was falling.

A correlation was shown only between rising pressure and ED activity during the nestling stage. Parman in Glick (1939) and Glick (1942) both stated swarming of some insects occurred during a rising pressure. A rising pressure at Edmonton, according to Professor Longley, generally indicates the passage of a low pressure system through the Edmonton region moving east and accompanied by strong northwest winds, cooler air and cloudy days, all indirectly influencing martin activity. The staff at the Department of Transport meteorology regional office at Edmonton stated that a rising pressure at this locality generally was accompanied by strong winds. As noted earlier strong winds reduced insect aerial numbers and therefore would explain the negative correlation between ED activity during the nestling stage and rising pressure.

Multiple Weather Factors

Following a consideration of the influence of each of the meteorological factors acting separately upon purple martin ED activity, I considered it desirable to examine the influence of combinations of these weather factors, upon ED activity. The method of analysis was described in Hardy and Milne (1938), but expanded to include three, and later four, meteorological factors acting in combination. In the analysis I considered temperature, wind velocity, sky opacity, relative humidity and barometric pressure per se. Pressure change influence was not studied because of insufficient data. Polygon figures used in the analysis are included in Appendices VI - XVIII.

Barometric pressure per se when combined separately with each of the other weather factors, appeared to have little or no influence upon ED activity in the nestling stage (Appendix VI). Because of this fact, barometric pressure was not considered further in the multiple analyses.

Results of an examination of the influence of paired meteorological factors upon purple martin ED activity are shown in Tables 11 and 12. The numbers in Table 11 represent the differences between maximum and minimum corner values of the polygons shown

Table 11. The relationship between purple martin ED activity during the separate divisions of the breeding cycle and meteorological factors taken in combination of two

Stages in breeding cycle		Difference between highest and lowest values at the corners of the polygon figures (see Appendices)							
		Temp vs sky opacity	Wind vs sky opacity	Temp vs wind	Wind vs relative humidity	Sky opacity vs relative humidity	Temp vs relative humidity	Mean and SD	Rank
Nest completion	8.6	6.3	6.1	6.2	5.6	4.3	6.2 ⁺ ₋ 1.3	1	
Post-breeding	6.7	8.1	5.9	3.9	4.1	5.7	5.7 [±] 1.4	2	
Nestling	4.4	5.6	4.5	4.8	4.3	3.6	4.5 ⁺ ₋ 0.6	3	
Nest building	3.9	2.4	5.4	4.4	4.2	3.5	4.0 [±] 0.9	4	
Arrival etc.	5.9	2.0	4.3	3.5	0.6	2.8	3.2 [±] 1.7	5	
Laying	4.2	3.1	2.0	2.7	2.9	2.7	2.9 ⁺ ₋ 0.7	6	
Incubation	3.2	3.3	1.8	1.9	3.2	1.5	2.5 ⁺ ₋ 0.8	7	
Mean and SD	5.3 ⁺ ₋ 1.7	4.4 [±] 2.0	4.3 [±] 1.6	3.9 ⁺ ₋ 1.3	3.6 ⁺ ₋ 1.4	3.4 [±] 1.2			
Rank	1	2	3	4	5	6			

Table 12. A second method for analyzing the relationship between purple martin ED activity during the separate divisions of the breeding cycle and meteorological factors taken in combinations of two

Stages in Differences between opposite sides of the polygon figures (see Appendices)														
breeding cycle	Temp vs sky opacity	Wind vs sky opacity	Temp vs wind	Wind vs relative humidity	Sky opacity vs relative humidity	Temp vs relative humidity	Mean and SD	Rank						
	T	SO	W	SO	T	W	RH	W	RH	SO	RH	T		
Nest completion	8.4	8.8	5.8	6.8	6.4	5.8	4.7	7.7	5.3	5.9	4.6	4.0	6.2 [±] 1.4	1
Post-breeding	9.3	1.7	1.7	8.9	10.6	1.2	3.8	3.6	7.2	0.2	9.8	1.6	5.0 [±] 3.8	2
Nestling	3.7	5.1	8.8	0.2	0.7	8.1	7.3	2.3	5.1	3.5	2.8	4.4	4.3 [±] 2.6	3
Nest building	1.6	2.6	2.1	2.7	1.9	3.1	2.9	3.9	2.1	3.3	0.6	3.8	2.6 [±] 0.3	4
Laying	1.5	4.9	0.8	5.2	1.6	0.2	1.0	4.0	3.9	0.9	0.3	3.3	2.3 [±] 1.8	5
Incubation	1.4	5.0	2.2	4.4	0.3	2.7	0.2	1.6	4.5	0.7	0.2	2.2	2.1 [±] 1.7	6
Arrival etc.	1.9	5.7	0.5	0.9	2.9	0.1	0.2	0.8	0.7	0.5	3.0	0.4	1.5 [±] 1.6	7
Mean	4.0	4.8	3.1	4.2	3.5	3.0	2.9	3.4	4.1	2.2	3.0	2.8		

Factor			Sum of Means		Rank	
Sky opacity	Temperature	Wind	Relative humidity	13.1	1	1
				10.5	2	2
Wind	Relative humidity			9.0	3	3
				8.4	4	4

in Appendices VII - XII. These values are considered as an expression of the influence of the particular pair of meteorological factors, when acting in combination, upon ED activity during that stage of the breeding cycle under consideration. Means of these numerical values were computed for ED activity in each stage. The ranked means indicate the relative order in which stages in the breeding cycle are influenced by weather. Table 11 shows that ED activity during the nest completion and post-breeding stages were influenced the most, whereas arrival, laying and incubation were affected the least.

To determine which pair of factors had the most influence upon activity, a mean was calculated for each pair of meteorological factors (Table 11). It is apparent that temperature and sky opacity had the most influence with the other factors somewhat less so.

Another method of analysing the paired factor influence upon activity is shown in Table 12. Numbers represent the difference between summed values on opposite sides of a polygon. Means of these differences were calculated for each stage in the breeding cycle and then ranked as shown. As is apparent the same general order of influence is shown in Table 12 as was seen in Table 11: ED activity during the

nest completion and post-breeding stages was influenced most; the laying, incubation and arrival stages were affected the least.

The data presented in Table 12 were used to determine which factor was most influential upon activity. Means for each factor were calculated and then totalled as shown. Sky opacity is shown to have the most influence upon ED activity and relative humidity the least.

After considering the influence of two meteorological factors, acting in combination, upon purple martin ED activity, three factors in combination were examined. Since temperature, sky opacity and wind velocity appeared to have the most influence upon activity, these three factors were combined together into a series of polygons as shown in Appendices XIII and XIV. The results of an analysis are shown in Tables 13 and 14. Data were treated similarly to those in Tables 11 and 12. It is apparent that when three factors are acting in combination, activity during the nest completion stage was influenced much more than during the other stages. The influence on the latter appeared to be about equal.

Table 13. The relationship between purple martin activity at the nest entrance during separate divisions of the breeding cycle and meteorological factors taken in combinations of three including temperature, sky opacity and wind velocity

Stage in breeding cycle	Differences between the highest and lowest values shown at the corners of each set of polygon figures	Rank
Nest completion	14.2	1
Post-breeding	9.4	2
Nest building	7.7	3
Arrival etc.	7.6	4
Nestling	7.0	5
Laying	6.1	6
Incubation	5.8	7

Table 14. A second method of analyses of the relationship between purple martin activity at the nest entrance during separate divisions of the breeding cycle and meteorological factors taken in combinations of three including temperature, sky opacity and wind velocity

Stage in breeding cycle	Differences between the sum of the highest values and the sum of the lowest values for each of the weather factors in each set of polygon figures	Rank
Nest completion	15.2	1
Nestling	8.4	2
Post-breeding	7.7	3
Laying	6.2	4
Incubation	5.6	5
Arrival etc.	4.6	6
Nest building	1.6	7

There was insufficient data to justify the complicated polygon analyses needed to consider four factors in combination and therefore I did not prepare a table as for two and three factors. However polygon figures were prepared for some of the breeding cycle stages to determine whether there was some influence of four factors in combination acting upon ED activity. An inspection of these figures as shown in Appendices XV -

XVIII indicated that days with low temperature, high sky opacity, wind velocity above 6.5 mph and high relative humidity resulted in the least ED activity. Most ED activity occurred when there was low sky opacity, wind velocity below 6.5 mph, relatively high temperature and low humidity.

A review of Tables 11, 12, 13 and 14 indicated that meteorological factors acting in combination had the greatest influence upon ED activity during the nest completion stage. This stage is one of transition between nest building and laying. The drive to carry nesting material has been satisfied but as yet the cavity contains no eggs or young. I presume that during clear, warm, calm weather sufficient food may be gathered in short order, leaving time for nest defence and a resultant increased ED activity. During dull, cool windy weather, martins spend relatively more time hawking insects which results in less time spent defending the nest site and a consequent reduction in ED activity.

ED activity during the post-breeding stage was second in the order of multiple factor influence. The polygon figures for activity in this stage show that high ED activity usually occurred on days when the temperature was low, the sky was overcast and the wind velocity was high, as opposed to lower activity under

opposite conditions. As discussed earlier martins in this stage may be affected by two physiological drives acting at the same time: feeding in preparation for migration and defending a future nest site in response to the stimulus of fall gonadal recrudescence. On days of "fair" weather birds are stimulated to feed; whereas on "poor" days birds defend the nest site.

Activity during the nestling stage was influenced by weather factors acting in combination. During this stage, I presume parental birds have a greater potential for a negative energy balance than at any other stage since they not only must feed themselves, but also nestlings. Warm, clear, calm days would result in abundant aerial insects (Hardy and Milne, 1938; Glick, 1939), with an increased rate of nestling feeding. On cool, dull, windy days insects are less numerous, consequently reducing the rate of feeding nestlings.

ED activity in the incubation stage was not influenced significantly by multiple weather factors. I assume this is so because of the establishment of a regular pattern of sessions and recesses during incubation (Skutch, 1962). If embryo development is to proceed, the eggs must be kept warm. It is only during extremely inclement weather, when adults are

forced into a prolonged search for food, that this session-recess pattern changes. In 1965 during three days of rain accompanied by cool temperatures, some incubating females left the nest for long periods of time, presumably in search of food. While they were away, English sparrows (Passer domesticus) entered the nests and destroyed some clutches.

ED activity during the arrival, nest defence, pair-bond formation stage was not influenced greatly by multiple weather factors. I postulate that during this stage the drive to locate and then defend and retain a nest cavity over-rides the influence of weather (barring extremes). Of the four male martins I had collected in the spring, each had a thick layer of fat which presumably could be utilized as a reserve energy supply. They would consequently not need to spend time feeding while they searched for and later defended a cavity.

Temperature and sky opacity are the most influential weather factors acting upon ED activity, as shown in Tables 12 and 13 and the polygon figures in the Appendices. Temperatures below 53°F substantially reduced activity. Martin ED activity on a day with clear to a half-over-cast sky was usually greater than on a completely over-cast day. Wind velocity was third in the order of in-

fluence. An examination of the polygon figures in the Appendices indicates a wind velocity above 6.5 mph usually caused a reduction of ED activity. Relative humidity was last in order of influence upon ED activity. Values of relative humidity above about 63 percent appeared to cause a slight reduction of ED activity. As mentioned earlier, higher relative humidities usually occurred on overcast, cool days and after some rain - all conditions which reduce ED activity.

REPRODUCTIVE CYCLE AND PRODUCTIVITY

The reproductive cycle in purple martins extends from the time birds first arrive in the spring until they depart in the fall. This period can be subdivided into seven stages. This subdivision was made on the basis of observations of activity at the nest boxes together with ED activity recorded by an Esterline Angus recorder.

Male purple martins may be separated into two age categories; those in adult plumage (Black in color), and those in first nuptial plumage (similar to females, brown in color) (Bent, 1942). Males in adult plumage will henceforth be called "adults" and males in first nuptial plumage will be called "yearlings". Both are sexually mature.

Arrival, Nest-Cavity Defence and Pair-Bond Formation

The first stage in the breeding cycle of purple martins was arbitrarily taken from the time of first defence of the nest cavity until nest building began. This stage is equivalent to the first three stages described by Allen and Nice (1952). I was unable to use their subdivision because of insufficient observational data.

Martins begin arriving at Edmonton in mid-April. The mean first arrival date over a 17-year period (1948-1965) was April 23 (M. Fisher pers. com.). By May 20 most adult birds have returned. Yearling males begin arriving in late May and are generally quite abundant by early June. The first yearling males were noted May 26, 1965 and May 25, 1966, at the experimental sites.

The level of ED activity is quite high at a martin colony during the first stage (Fig. 2, A and B). Males are continually entering and leaving the nest cavity, while defending it against other males and attempting to attract females (Gaunt, 1959; Johnson and Hardy, 1962). ED activity was generally greater in the morning than in the afternoon, given optimum weather conditions (Fig. 2, A and B). The reduced ED activity on June 8 presumably was caused by a relatively high mean wind velocity of 10 mph for the day, whereas on

June 9 the mean wind velocity was 5 mph, and on June 11, 8 mph, other weather conditions were relatively the same on all 3 days. June 10 was not used because of 6 hours of rain in the morning and 3 hours in the afternoon which substantially reduced ED activity. The reduced activity shown in Figure 2, B, on June 20 and June 22 was presumably the result of a general reduction in nest defence activity in the colony since most pairs were incubating by this time.

Based on the data for 21 pairs, the first stage in the breeding cycle lasted 6.5 ± 7.1 days with a range of less than one day to 30 days. In 1966 birds that arrived before May 25 took a mean of 5.4 days, whereas later arrivals spent a mean time of 2.0 days in this stage. The pair that spent 30 days in this stage was the first to arrive at the colony in 1965. After the first day, April 28, they remained associated with one cavity and were apparently mated. They did not begin building a nest until 6 of the 8 pair in the colony had arrived and three other pair had begun nest building. This pair began laying about the same time as did the others.

A typical ED activity pattern for this first stage, but condensed into a 4-day interval between June 20 and June 23 inclusive, is shown in Figure 2, B. A yearling

male was seen to arrive at 0700 hours on June 20. It attempted unsuccessfully to occupy a central nest cavity but was driven away by an adult male occupying an adjacent cavity. At 1200 hours, during a subsequent half hour period of observation, a yearling male was in complete possession of this central nest cavity. No data were recorded over the noon hour because of colony examination. Later, data were not recorded for the next 30 hours because of electronic difficulties. A yearling male was observed defending this cavity on June 21 and June 22. By this date there were very few males searching for nest cavities, which would explain reduced ED activity shown on June 22. At 0700 hours on June 23, a female was resting in the nest entrance. Presumably they were forming a pair-bond as the male was rapidly entering and leaving the nest cavity. This activity would explain the increase in overall ED activity throughout June 23, since weather conditions were comparable to those of the day before. On June 24 nest building began.

It appears that after martins arrive, some time is spent defending the nest cavity prior to building a nest. This period is shortened after about May 25. Late arriving pairs acquire a cavity and very shortly begin nest building.

Nest Building

The nest building stage commences with the appearance of material in the cavity and terminates when the nest cup is lined with green leaves. This period is equivalent to the first part of "Stage 4" of Allen and Nice (1952).

Nest building took a mean of 11.8 days in 1965 and 1966, with a minimum of 5 and a maximum of 27 days. Table 15 presents the pertinent data.

Table 15. Distribution of time periods required for the nest building stage in the breeding cycle of purple martins in 1965 and 1966 at Edmonton, Alberta

Days spent																			Mean no. days
nest building	5	6	7	8	9	10	11	12	13	14	15	18	21	22	27				
Yearling		2	3	2	1	1											7.6		
Adult		1	1			2	3	3	2	3	2	1	1	1	1		13.6		
Total		1	2	4	2	1	3	3	3	2	3	2	1	1	1	1	11.8		

These periods compare favourably to those reported by Allen and Nice (op cit). Birds that were late in acquiring a cavity built their nests in the shortest time. Almost all late nesters were yearlings. A mean of 7.6 days was shown for yearling birds, whereas adults took 13.6 days to build the nest. The long period of 27 days was by a relatively-early-nesting pair.

The influence of the electronic equipment on the time involved in the nesting stage was investigated by comparing the control and experimental nests. No significant difference, using the Wilcoxon Two-Sample Test (Alder and Roessler, 1964), was found.

Observations indicated that most nest building took place in the morning. This agrees with the greater overall ED activity shown in the morning (Fig. 2, C). Observations in the afternoon indicated birds generally were not around the colony.

Activity at the nest entrance during the nest-building stage was characterized by periods of nest construction lasting a few minutes and then periods with no activity when birds were away from the colony.

ED activity recorded during the nest-building stage was only exceeded by activity in the previous stage (Fig. 2). ED activity shown on May 29 represents the relatively high levels of intensity during fair weather. Reduced ED activity on May 27 presumably was due to high wind velocities (a mean of 18 mph). The lower temperatures (mean of 51°F) on May 28 caused the reduction of ED activity.

Nest Completion

The nest completion stage covers the time interval between the day the nest cup is lined with leaves and the day laying begins. This period corresponds to the latter part of Allen and Nice's (1952) "Stage 4".

Nest completion lasted a mean of 3.2 days with a range of 0 to 9 days (Table 16). This time interval compares favourably with the 3 days reported by Purchon (1948) for European swallows (Hirundo rustica). The shorter periods of time generally involved late nesting birds. The period of 9 days was shown by a pair which took early possession of a nest cavity and began nest building within a week. Presumably the nest was finished before the female was physiologically ready to lay.

Table 16. Distribution of time periods for the nest completion stage by purple martins in the Edmonton area, Alberta

Periods of time in days for nest completion										
Days	0	1	2	3	4	5	6	7	9	Mean
No. of Pairs	7	1	5	3	1	4	3	1	2	3.2

There was no significant difference between experimental and control nests for the time spent in the nest completion stage.

Total ED activity during the nest completion stage was slightly less than during the previous stages (Fig. 2, D). At this time males continued to defend the nest but observations indicated there was little competition for nest sites. On June 5 the colony was disturbed for 18 minutes near 0830 hours which probably caused the sharp decrease in activity. The colony was also disturbed for 18 minutes at 1800 hours on June 8. Weather conditions were comparable for all three days.

A foreshortening of the nest building and nest completion stages occurred as the season progressed (Table 17).

Table 17. Weekly comparison of the termination of nest building and nest completion stages for purple martins at Edmonton, Alberta

Date of first egg	Mean* in days	1965		Mean* in days	1966		Mean* in days	Total	
		Range* in days	No. of nests		Range* in days	No. of nests		Range* in days	No. of nests
May 29- June 4	20		1	14.3	13-16	3	15.8	13-20	4
June 5- June 11	11.7	10-15	3	16.6	12-23	3	14.2	10-23	6
June 12- June 18	11.5	8-15	2	14.9	7-27	14	14.5	7-27	16
June 19- June 26	12		1	6.3	5-8	3	7.8	5-12	4
July 10	7		1				7		1

* Time in days from beginning of nest building until first egg appears.

The interval required for late nesting birds is substantially reduced late in the season. This may be an adaptation to assure that young hatch when aerial insects are most abundant in late June and July (Dr. B. Hocking and Dr. G.E. Ball, pers. comm.).

Laying

Purple martins generally lay in the early morning on successive days (Allen and Nice, 1952).

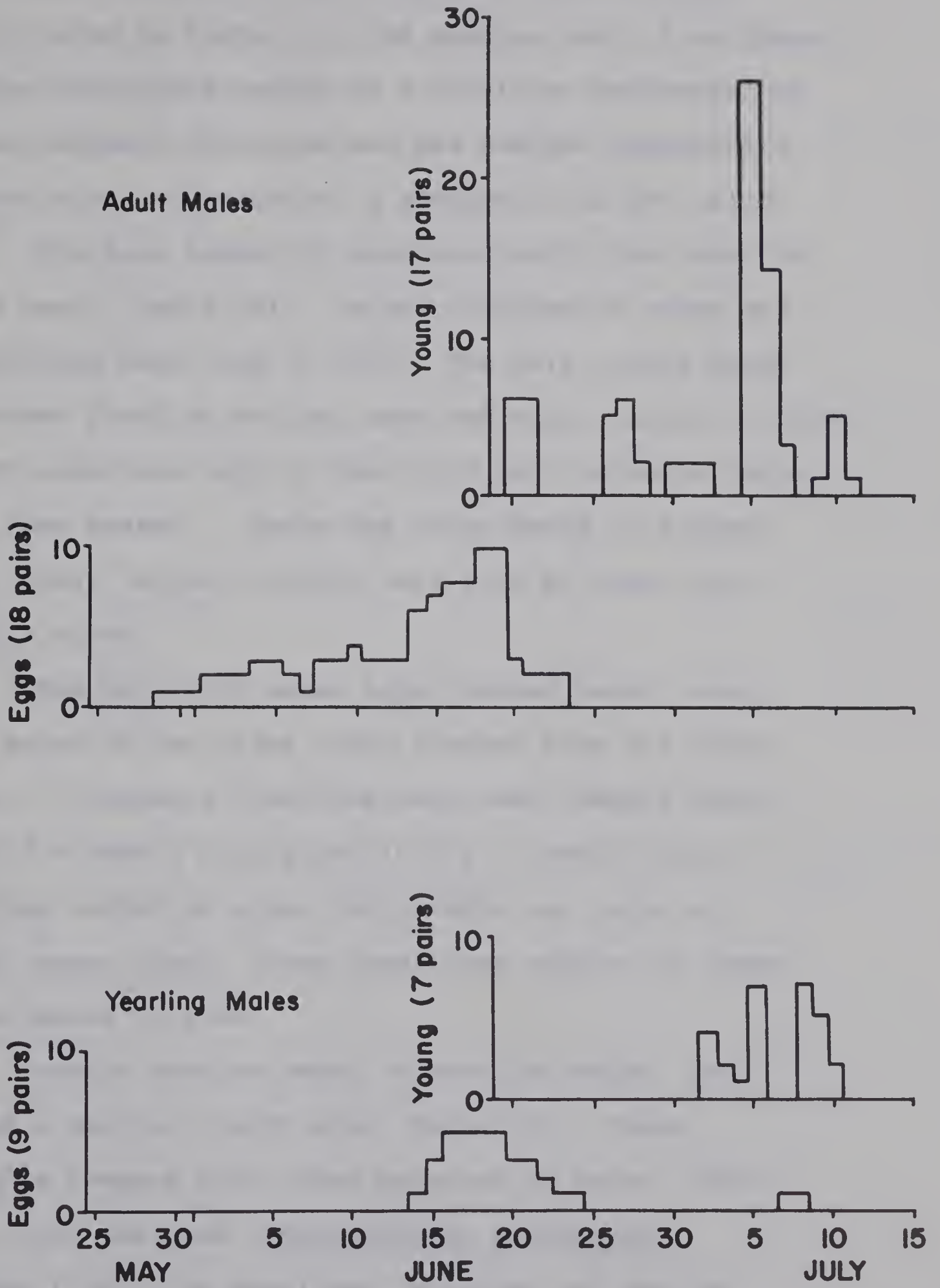
Female martins mated to adult males began laying up to two weeks before those mated to yearling males (Fig. 7). Adult birds arrived between late April and mid-May, whereas yearling males did not arrive until late May. Both age groups commenced nest building shortly after arrival. The later the arrival, the less time spent in the early stages of the breeding cycle. This reduction in time explains the close agreement of peak laying for both age groups as shown in Figure 7. The skewed distribution for adults may be explained by some birds arriving early and beginning to nest immediately. The fact that the curves for hatching differ from those for laying is because all eggs in a clutch hatch synchronously.

Martins, in the Edmonton area, laid 4.8 ± 0.6 eggs (Table 18). This number of eggs approaches closely that reported by Widmann (1922) of 4.9 and Allen and Nice (1952) of 4.9 ± 0.7 . It appears that purple martins, nesting near the northern limits of their range, have not changed their clutch size.

MacArthur (1961: 196) claims that "if, due to severe climate and the hazards of longer migration, mortality

Figure 7. A comparison of the laying and hatching dates between female purple martins mated to males in adult plumage and those in yearling plumage in the same colony, Edmonton area, Alberta

NUMBER OF NEWLY LAID EGGS AND NEWLY HATCHED YOUNG



is always greater at high latitude, then so must clutch size be higher, or the species won't live there." Either the purple martin is a relative "new comer" to these northern latitudes and has not yet adapted its clutch size, or MacArthur's assumption is not valid.

The mean number of eggs was nearly the same for both years (Table 18). Larger clutches of seven and eight eggs were laid in 1966. The pair laying seven eggs was first to arrive, nest and begin laying in 1966. Eight eggs were laid by the third pair to begin laying the same season. There was no evidence to suggest that these larger clutches were laid by other than single birds.

The pair with seven eggs fledged seven young, and seven of the eight young fledged from the other nest. It appears from this very small sample that should a female purple martin lay a greater than average number of eggs, the parents can raise at least seven young, given conditions similar to those experienced in 1966.

Female martins mated to yearling males, produced a smaller clutch size (Table 18). These results compare with those reported by Meyer (1957) for cliff swallows (Petrochelidon pyrrhonota); Kuroda (1964) for starlings (Sturnus) and Perrins

Table 18. Distribution of purple martin clutch sizes in the Edmonton area, Alberta

Year	Purple martin pairs	Clutch size						Total	Mean and SD
		Age of male			Number				
		<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>	<u>7</u>	<u>8</u>		
1965	Yearling	1	1	2				4	4.25 [±] 0.4
	Adult	1	5*	11	3			20	4.80 [±] 0.83
	Total	2	6	13	3			24	4.71 [±] 0.79
1966	Yearling	1	5	4				10	4.30 [±] 0.71
	Adult	2	2	9	5	1	1	20	5.80 [±] 1.16
	Total	3	7	13	5	1	1	30	4.90 [±] 0.99
1965 and 1966	Yearling	2	6	6				14	4.29 [±] 0.67
	Adult	3	7*	20	8	1	1	40	5.00 [±] 0.63
	Total	5	13*	26	8	1	1	54	4.81 [±] 0.61

* Includes 3 replacement clutches

(1965) for great tits (Parus major); Lee (1967) for purple martins. Presumably the reduction in clutch size by female martins mated to yearlings, which generally began nesting later than those mated to adults, would shorten the total time for the breeding cycle and hence nestlings would hatch out one or two days earlier than if the clutch had been of larger size.

A comparison between the date of onset of laying

and clutch size is shown in Table 19. It is apparent that clutch size was diminished as the season progressed. In addition the daily number of newly-laid eggs and newly hatched young are presented for the years 1965 and 1966 in Figure 8.

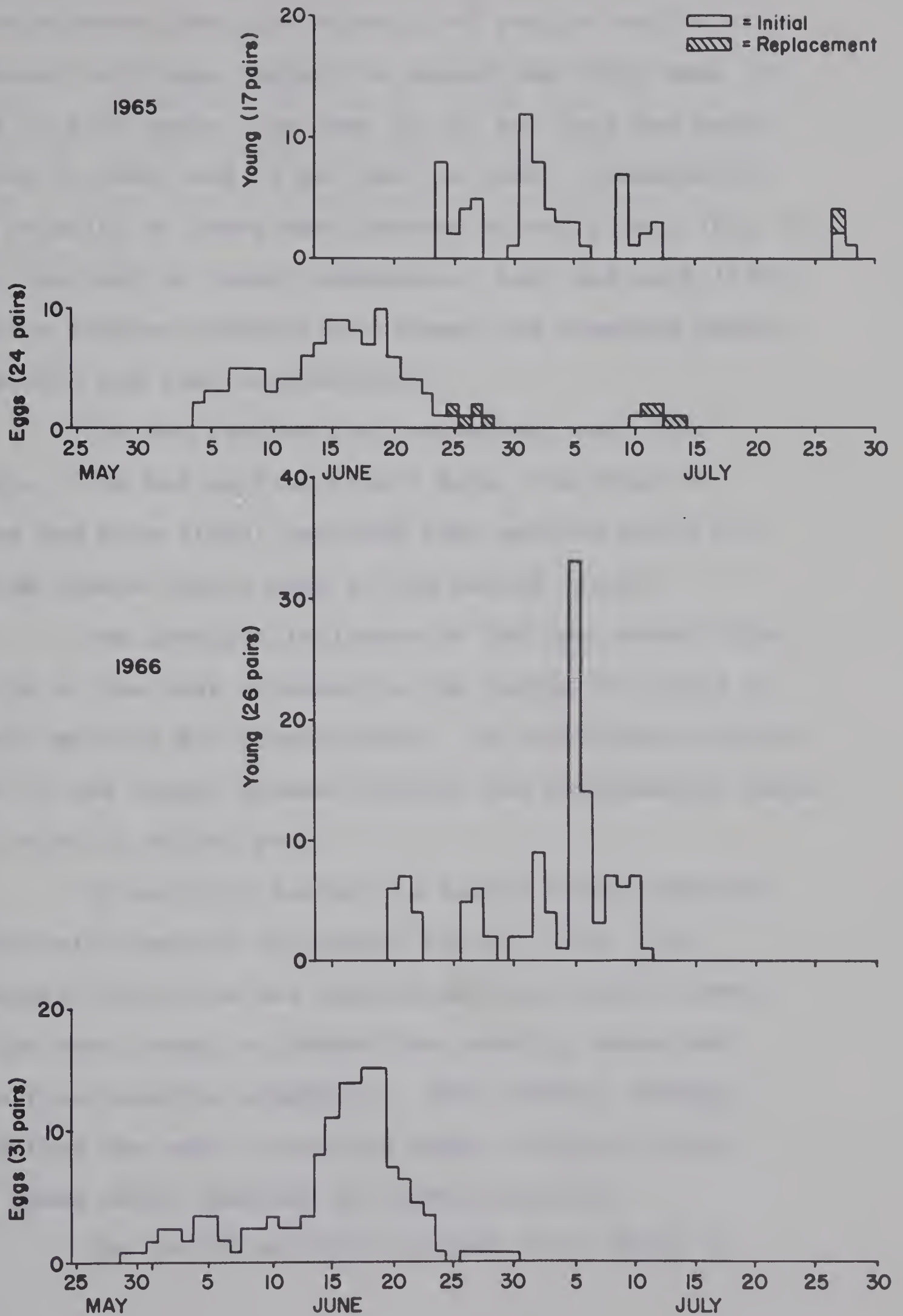
Table 19. Clutch size in purple martins, in relation to the onset of laying in the Edmonton area, Alberta

Year	First egg laid in week ending	Number of clutches	Cumulative sum % of total	Clutch size	
				Mean	SD
1965	June 4	2	8.3	6.00 \pm 0	
	June 11	5	29.1	5.20 \pm 0.40	
	June 18	9	66.6	4.78 \pm 0.42	
	June 25	5 *	87.4	4.20 \pm 0.75	
	July 2	0			
	July 9	1 *	91.6	4.00	
	July 16	2 *	100.0	3.50 \pm 0.50	
	All pairs	24 *		4.71 \pm 0.79	
1966	June 4	4	13.3	6.25 \pm 0.42	
	June 11	3	23.3	5.33 \pm 0.15	
	June 18	19	86.7	4.63 \pm 1.00	
	June 25	3	96.7	4.33 \pm 0.15	
	July 2	1	100.00	5.00	
	All pairs	30		4.90 \pm 0.99	

* Includes replacement clutches

Figure 8. Laying and hatching frequencies for purple martins in the Edmonton area, Alberta

NUMBER OF NEWLY LAID EGGS AND NEWLY HATCHED YOUNG



It is apparent that the majority of purple martins at Edmonton laid eggs during the second and third week of June in both years. By June 25, 87 per cent had begun laying in 1965, and 97 per cent in 1966. Consequently the majority of young were hatched by early July (Fig. 8) near the peak of insect abundance. Lack and Lack (1951) found a similar correlation between the breeding season of swifts and food availability.

The two females that re-nested, each laid 4 eggs. One had earlier laid 6 eggs, the other 5. Allen and Nice (1952) reported that martins which re-nested always laid 4 eggs in the second clutch.

The possible influence of the continuous light source at the nest entrance on the timing of laying in purple martins was investigated. No significant difference in the timing between control and experimental nests was found in either year.

ED activity during the laying stage remained relatively constant throughout the day (Fig. 3,A). I suggest that this was because martins stayed closer to the nest, ready to defend the recently deposited eggs from possible predation. This greater tendency to defend the nest, once they began to deposit eggs, was noted while checking the nests each day.

The low ED activity on June 12 as shown in

Figure 3, presumably was due to a high mean wind velocity of 13 mph, as compared to 10 mph on the other two days shown. Other weather conditions were comparable on all three days.

Incubation

The period of incubation is the time from the laying of the last egg in a clutch until it hatches (Thomson, 1964). To determine this time, I selected, in 1965, 11 nests and numbered each egg on the day it was laid. In one nest, the last egg hatched at the same time as the others; in two nests it hatched with the last part of the clutch; and in eight nests it was the last egg to hatch.

The mean incubation time for the marked eggs was 16.6 days, the same as that for all nests in both seasons (Table 20). This time is slightly in excess of that of 15 to 16 days reported by Allen and Nice (1952). I presume the greater length of time is due to the cooler climate of the more northern latitude at Edmonton. Edmonton has a mean temperature in June of 57.8°F , whereas at Ann Arbor, Michigan, the site of Allen and Nice's (1952) investigation, it is 67.9°F . When a female departs to feed while incubating she allows the eggs to cool and embryo development is retarded.

There was no correlation between either clutch size or age of males and length of incubation time. The mean incubation time for clutches in control and experimental nests was not significantly different.

Table 20. Distribution of time periods for the duration of incubation for purple martins in the Edmonton area, Alberta

	<u>Days</u>				<u>Mean</u>
	<u>15</u>	<u>16</u>	<u>17</u>	<u>18</u>	
Nests with marked eggs		6	3	2	16.6
1965, 1966 totals	1	19	15	6	16.6

ED activity during the incubation stage is shown in Figure 3, B. The three days selected include the first day of incubation, a day near the middle of the stage and a day near the end. On the afternoon of June 17, the decrease in activity coincided with cool weather accompanied by rain, as did the decrease late on the afternoon of June 22. June 29 was warm and sunny all day, and ED activity remained at about the same level throughout. It appears that female birds have certain sessions and recesses while incubating, and unless there is extremely inclement weather, ED activity remains relatively constant.

Nestling

The nestling stage extends from hatching of the last egg to fledging of the last young. Purple martins remained in the nest approximately four weeks. The mean departure time for 15 broods studied was 27.4 days ranging from 26 to 31 days (Table 21). There was no difference in departure time between 1965 and 1966, and consequently the data for both years were combined. In one nest not included in this table, a nestling remained 37 days in the cavity. The four siblings from this nest had left an unknown number of days earlier. This individual was examined and showed no observable defects. The parents continued to feed it until it departed.

Table 21. Distribution of time periods for the nestling stage in purple martins at the experimental boxes in the Edmonton area, Alberta

Number of young fledged	Number of broods	Number of days until all young fledged				
		<u>26</u>	<u>27</u>	<u>28</u>	<u>29</u>	<u>31</u>
1	1					1
2	1			1		
3	5	2	3			
4	2		1	1		
5	3	2				1
6	2		1		1	
7	<u>1</u>	<u>1</u>				
Total	15	5	5	2	1	2

Reports in the literature indicate that martins remained in the nest elsewhere slightly longer than at Edmonton. Forbush (1929) stated that martins sometimes remained in the nest for six weeks. Allen and Nice (1952) found martins fledged at between 27 and 35 days, usually about 28. The earlier fledging at Edmonton may be due to more hours of sunlight at this northern latitude which would provide more feeding time and presumably faster growth.

Between day 17 and 21 of the nestling stage, the young came to the nest entrance to beg and accept food. A mean of 19.6 days was calculated for this time with a range of 14 to 24 days (Table 22). There was no difference between the data collected in 1965 and 1966 and between control and experimental nests. The data were consequently combined.

To follow growth of the young, wing chord measurements were made of nestlings in two nests with three young, and three nests with five (Figs. 9 and 10). The curves were prepared using the known age of each young in the nest. Nestlings had been individually marked on hatching. From about the 5th day onward one or more nestlings had longer wings than the others. These larger nestlings were assumed to be males as adult and yearling males were found to be the same size

Figure 9. A growth curve of wing lengths in purple martin nestlings based on two nests each containing three nestlings in 1965 at Edmonton, Alberta. Curve was drawn by inspection.

SIZE OF PARENT BIRDS

Males		Females	
Adult	○	Yearling	▲
			○

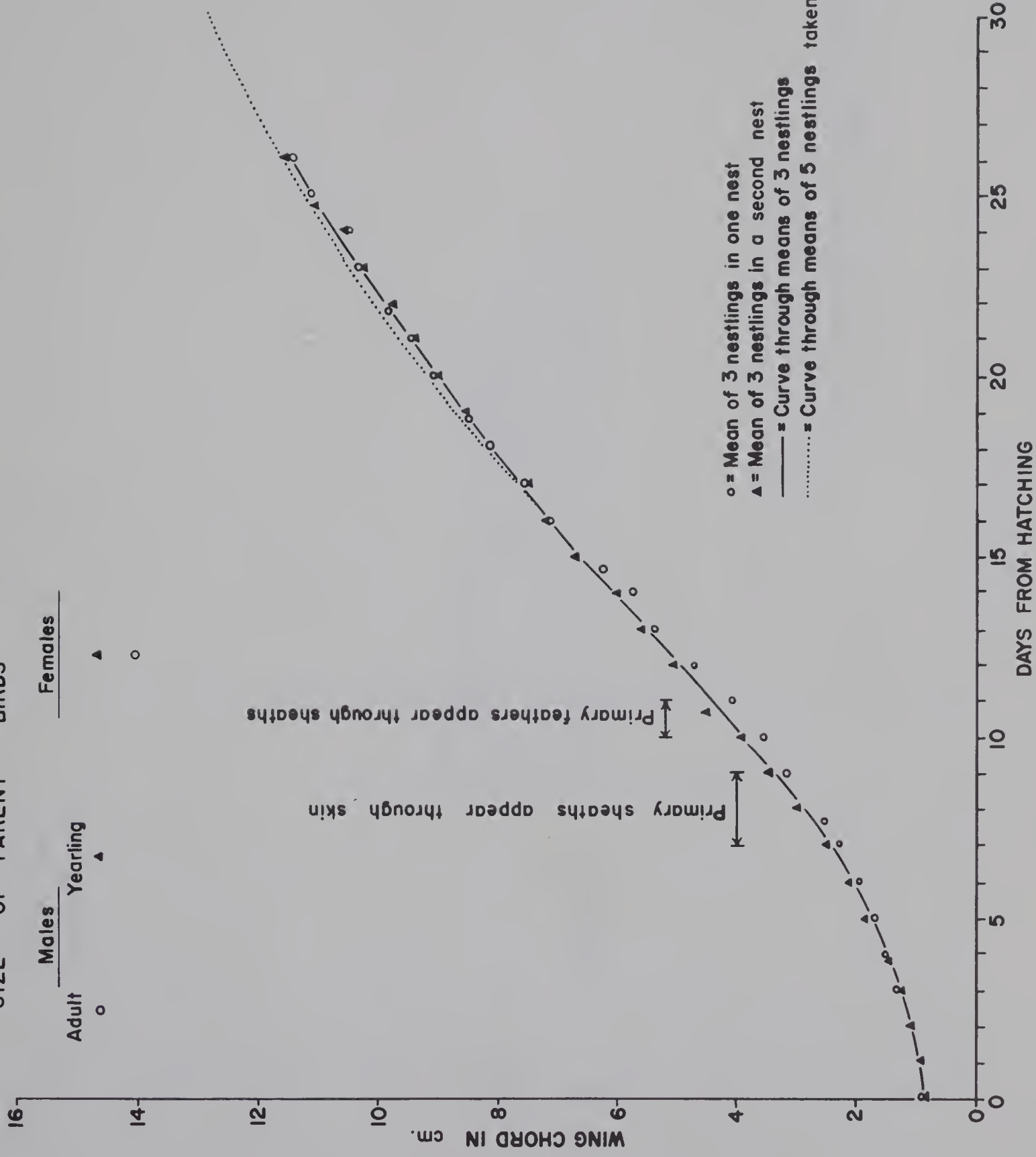


Figure 10. A growth curve of wing lengths in purple martin nestlings based on three nests each containing five nestlings in 1965 at Edmonton, Alberta. Curve was drawn by inspection.

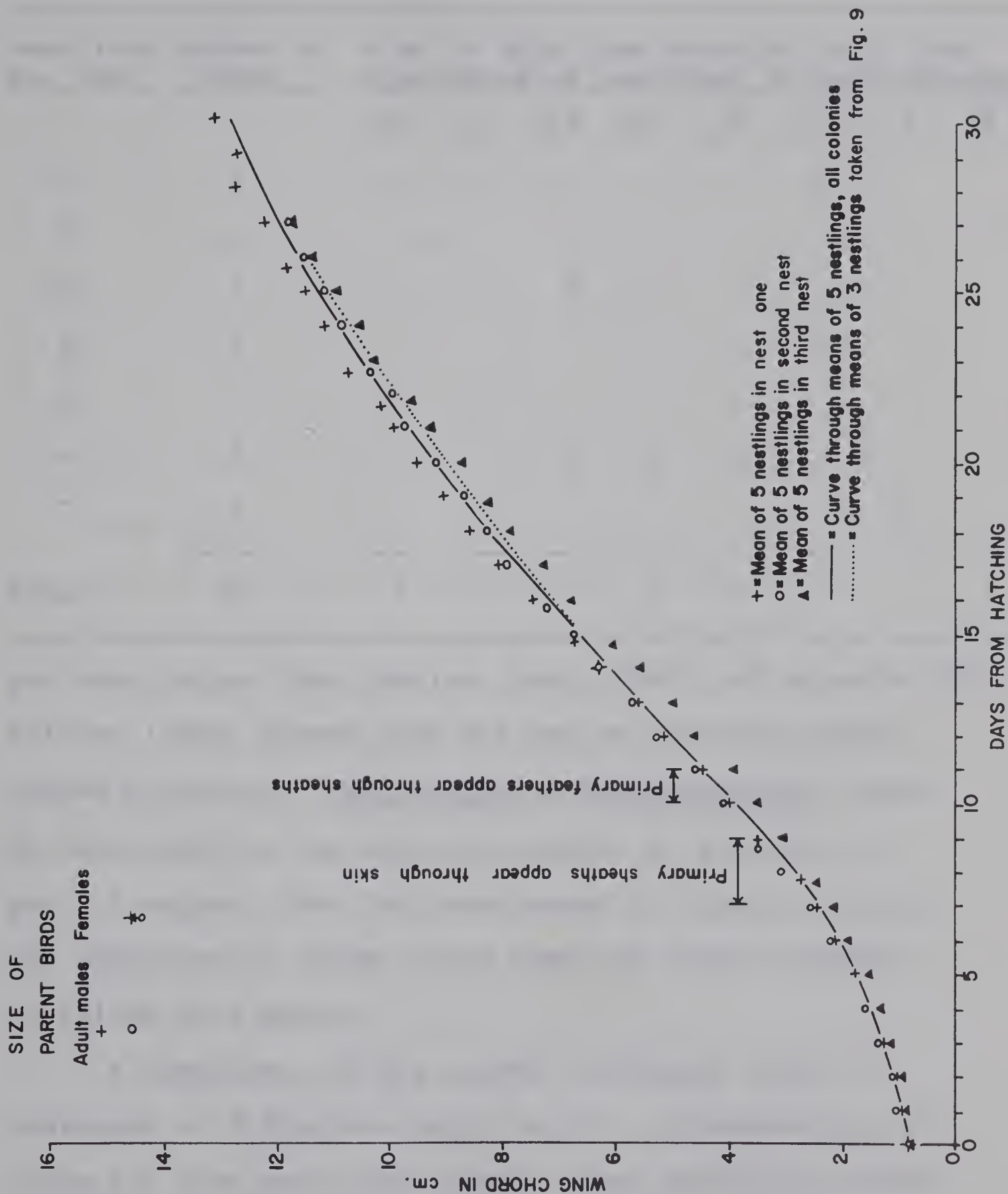


Table 22. Distribution of time periods prior to the appearance of nestlings at the nest entrance

Nestlings per nest	Number of nests	Time in days from hatching until the appearance of nestlings at nest entrance							
		<u>14</u>	<u>17</u>	<u>18</u>	<u>19</u>	<u>20</u>	<u>21</u>	<u>23</u>	<u>24</u>
1	1						1		
2	1								1
3	6			2	1	3			
4	5					3	2		
5	7	1	1			5			
6	4			1	1	2			
7	2		1					1	
Total	26	1	2	3	2	13	3	1	1

and were larger than females (Bent (1942) and Appendix XIX). Willson (1966) showed that the sex of nestling yellow-headed blackbirds (Xanthocephalus xanthocephalus) could be determined on the basis of weight, at six days of age. I suggest that the brood shown in Figure 10 which had consistently larger young than the others probably contained more males.

A comparison of the curves in Figures 9 and 10 indicated no difference until day 17. Subsequently the curve for five nestlings showed larger nestlings present. This could be explained by more males per brood in the nests with five young.

It was observed that the appearance of the primary feather sheaths and later the primary feathers had no influence on the growth curves.

The number of young martins fledged at Edmonton was greater than found in other studies, even though the clutch size was the same (Table 23). Martins studied at more southern latitudes were influenced by rain and cold weather which reduced their numbers. One period of bad weather at Edmonton occurred when most birds were incubating. Of the four nests with young at this time, all lost at least one chick and one lost three of five. I presume that if weather conditions during this study had been as detrimental as described in the reports from more southern areas, then martin productivity would have been substantially reduced.

ED activity as shown in Figure 3, C, together with observations, indicate that nestling feeding began in the early morning, continued at a steady rate all day, and fell off at or near sunset. There did not appear to be any major peaks or troughs in levels of activity. Once the adults begin feeding nestlings they apparently continue at about the same rate.

Allen and Nice (1952;635) had stated, "It seems evident that both age and number of young influence the rate of feeding although we are hampered by lack of exact information on both these points". This

Table 23. A comparison of purple martin productivity at Edmonton Alberta with that reported at three colonies in the U.S.A. as reported by Allen and Nice (1952). The Pennsylvania figures are estimates

<u>Location</u>	<u>Years of study</u>	<u>No. of nests</u>	<u>No. of eggs laid</u>	<u>Nestlings</u>		<u>Fledged per pair</u>			
				<u>Total</u>	<u>Mean per nest</u>		<u>Hatched</u>	<u>Fledged</u>	
							<u>No.</u>	<u>%</u>	<u>No.</u>
Michigan	3	29	143	4.9	119	83.2	55	31.5	1.9
Missouri	1	45	220	4.9	129	58.2	110	50.0	2.4
Pennyslvania	7	294	1380?	4.7?	1100?	80.0?	850?	61.6?	2.9?
Alberta	2	55	262	4.8	198	76	185	70.7	3.4

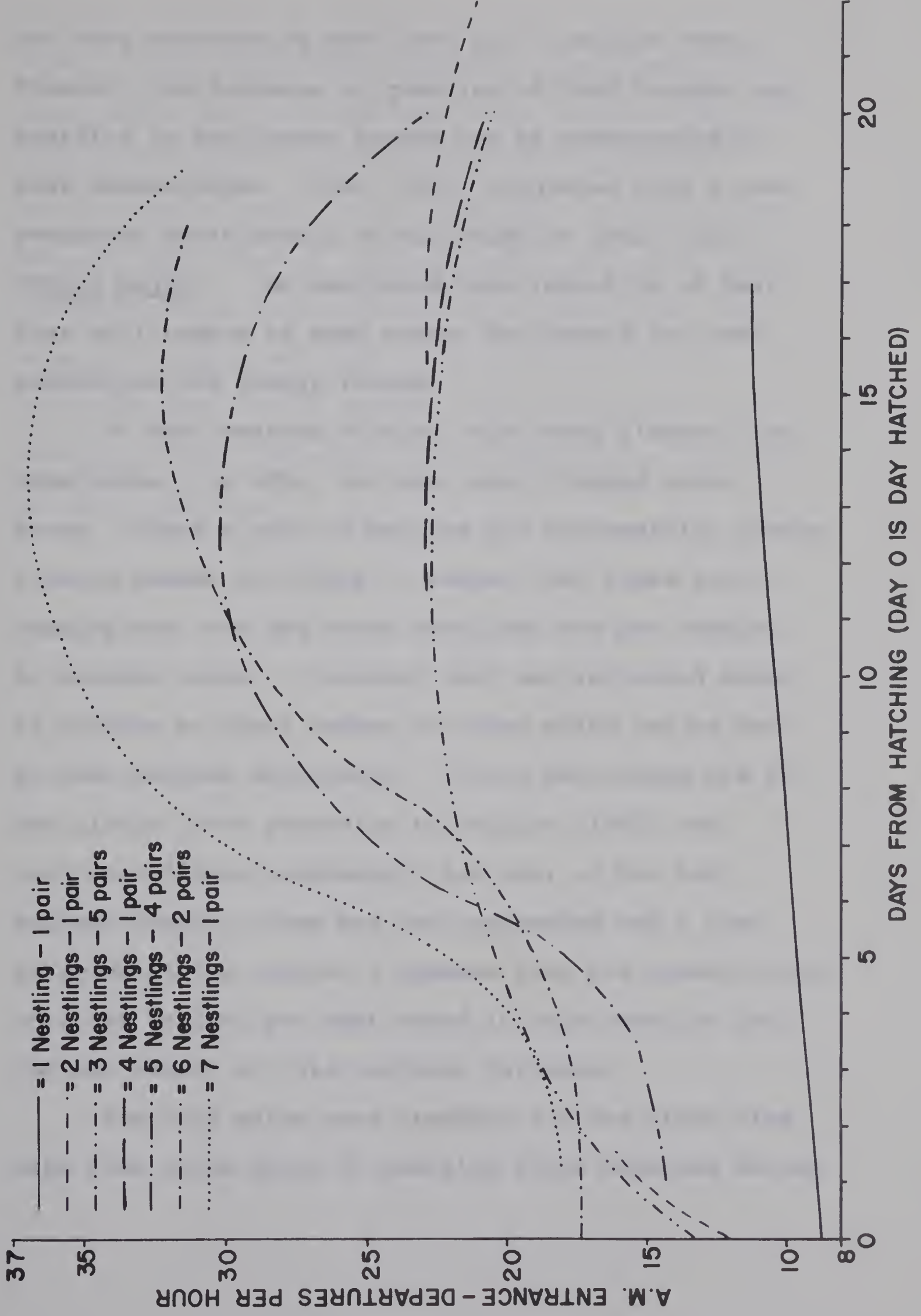
speculation was investigated. It appears from Figure 11 that ED activity, presumably the rate of feeding, increased both with the age of young and the number per nest. The activity curve, for all broods with more than one nestling rose to a plateau at about day 10 and remained at this level until day 14, when ED activity began to decrease. An increase in number of trips per hour as the nestlings aged was similarly reported for other swallow species (Moreau, 1939, 1940; Purchon, 1948).

The decrease in number of feeding trips per hour after day 14, coincided with observations of adults bringing to the young much larger insects including *Odontata* and *Lepidoptera* of unknown species. Observations indicate that the number of trips with larger insects increased as the young become older. Parental feeding trips could be reduced and yet still provide the same amount of potential energy per nestling.

Various workers have reported that the number of feeding trips was greater in larger broods but not proportional to the brood size (Nice, 1943; Moreau, 1947; Lack, 1948, 1954; Gibb, 1955; Royama, 1966; Willson, 1966). My results agree with these findings (Fig. 11). Each young in larger broods presumably would

Figure 11. Mean morning activity on a per hour basis for each day during the nestling stage for nests containing one to seven young.

Curves were drawn by inspection and were prepared, ignoring data recorded on days with very cold, windy, rainy weather.



not have received as much food as in smaller ones. Possibly the decrease in quantity of food brought per nestling in the larger broods may be compensated by heat conservation. Gibb (1955) suggested such a compensatory relationship in his study of great tits (Parus major). He mentioned that reduction of heat loss will reduce to some extent the demand for heat production and energy intake.

In both seasons studied, six young fledged from some nests. In 1966, two pair each fledged seven young. Since a pair of martins can successfully fledge a large number of chicks, I assume that those pairs feeding one, two and three nestlings are not feeding at maximum rates. I suggest that martins would adapt to produce an ideal number of young which can be fed at near maximum efficiency. If too many young are in the clutch, then according to Perrins (1965) the nestlings fledge underweight and die; if too few, maximum feeding rates are not approached and a loss of productivity occurs. I presume that the productivity of three to four per nest found in this study is the optimum number at this northern latitude.

Yearling males were breeding for the first time. Data from three pairs of yearling birds obtained during

three, 3-hour observation periods a week apart with young about one, two and then three weeks of age, indicated that the yearling males fed nestlings 45 per cent as often as did females at the same nest. Whereas data from six to seven pairs with adult males, obtained at the same time and with young about the same age, indicated adult male trips to the nest equalled those of the female at the same nest. Kendeigh (1952) reported similar results for one pair of adult martins.

Post-Breeding, Nest-Cavity Defence

The post-breeding nest-cavity defence stage lasts from the time nestlings begin to fledge until birds depart on fall migration.

The post-breeding stage is not as well documented as are the stages of the breeding cycle. Allen and Nice (1952) in their excellent study do not mention it. Olmstead (1955:8) briefly discusses this stage by stating that "After the young are fledged, adult males engage in short decisive flights and sing short bursts of song from the ledge of the box. A few mated pairs linger near the nest but females and young are in the minority." Johnston and Hardy (1962) mention groups of 3 or more individual martins participate as social units in investigating neighbouring colonies in the spring and after completing breeding. Researchers have reported fall activity for other bird species: Brewster (1925) and Bump et al (1947) mention fall drumming of ruffed grouse (Bonasa umbellus); Nice (1937) mentions young resident song sparrows (Melospiza melodia) taking up territory in their first fall; Morley (1943) summarized the European literature on bird territorial activity in the fall; Peterson (1955) observed recently fledged bank swallows examining old holes and digging at new ones.

I first observed post-breeding nest-cavity defence activity at Edmonton in 1963. That season a nest box that had gone unused all summer was, for about a week in early fall, the scene of intensive ED activity by several yearling males. The same procedure was noted the next season, and in 1965 and 1966 it was recorded with the electronic equipment at the experimental sites. In 1966, a new phase was noted - at least three yearling males attracted females which assisted in defending the cavity for several days.

Based on data for 14 males, the final stage in the breeding cycle lasted 5.9 ± 4.6 days with a range of one to 19 days.

Activity during the post-breeding stage was quite intense as shown in Figure 3, D. Recorded ED activity together with observational data indicated there were two daily peaks of activity - morning and afternoon. The former was generally greater. A comparison between activity in the first and last stages (Figures 2, A and 3, D) shows that post-breeding ED activity is just as intense as shown for the arrival stage.

An example of ED activity in the last stage is shown in Figure 3, D. An unmated yearling male was first noted at a nest cavity which contained seven young on July 12. The yearling male sat on the nest

porch while the adult male and his mate busily fed the seven nestlings. This yearling male was not seen to feed the nestlings during several short watches ranging from about 10 minutes up to about an hour and one 3-hour period. By July 18, the young had fledged. Little ED activity was recorded for several days. On July 23, a yearling male was noted at this nest participating in post-breeding nest-cavity defence behaviour. Activity continued each morning on the same high level of intensity and on July 27, a female joined him. Both sexes then participated in defence of the cavity. On July 30 at 1000 hours an adult male had apparently displaced the yearling pair which had been present the afternoon before. A yearling male, possibly the same bird, was back by at least the morning of August 1. Activity began to decline, and by August 9 it had virtually stopped.

Observation of color banded birds indicated previous nest tenants that have fledged young did not appear to participate in this stage.

In view of the lack of a detailed description in the literature of post-breeding nest-cavity defence by purple martins, I include the following account. Post-breeding activity began in the early morning with males, usually yearlings, arriving at the nest

boxes either singly or in small flocks. Some individuals entered the nest cavities without hesitation, others, which I presumed were newcomers, hesitated before entering the cavities. The occupant of a cavity defended it by making sudden outward lunges from the entrance, or by resting in front of the nest entrance. Nest material was not observed being gathered during the post-breeding stage.

During this stage, birds were continually flying from cavity to cavity. If a new bird arrived all established males would produce a piercing cry, attempting to discourage the newcomer from landing nearby. Few fights were observed.

Intensity of post-breeding defence increased as the season progressed. By the time the last young fledged in 1966, between 30 to 40 martins were competing for possession of future nest cavities. This competition continued for a few days and then ceased by August 2, in both years.

I suggest that post-breeding defence activity helps to imprint upon participating birds the location of future nest sites. A territory is learned to which they will return the following spring, and consequently have the same advantage in nest findings as the birds which had previously nested. Martins have an extremely

good homing instinct. Southern (1959) found that all of 16 birds released from 1.72 to 235 miles returned. The bird released farthest away returned in 8.6 hours. Data from birds banded in this study indicated martins return each year to nest in the same area. Observations suggest they "remember" the exact location of nest boxes, since in the spring, if the box has not yet been put up, they will flutter around where it was the previous year. Nice (1937) has shown that territorial behaviour in the song sparrow in the late summer has the function of fixing in the bird an individual territory to which it later returns in the spring. Similarly, purple martins may learn the location of available nest sites by post-breeding activity. By the time they depart on migration I suspect most possible nest sites are known within a radius of 10 miles. Returns of banded yearlings indicate that they nested from three to ten miles from the home colony. This knowledge of available nest sites may even extend farther, since one female nested 85 miles southwest of the place where she was raised.

GENERAL DISCUSSION AND CONCLUSIONS

The influence of weather on the size of animal populations has been discussed in the literature. Birch (1957:106) states "weather is a component of the environment of animals which effectively determines the limits to distribution and the abundance of some species. Short term and long term changes in weather determine short term and long term changes in distribution and abundance". This approach is opposed to the density-dependent concept, which supposes that populations are permitted to grow when densities are relatively low and prevented when densities are high. Nicholson (1957), taking a more realistic approach, stated that the density of a population is not governed by biotic and abiotic factors per se but by such attributes of these elements as availability, accessibility, intensity, etc. Furthermore, he states that inherent in all populations is "the ability to adjust themselves to great changes in their environments". Purple martin populations do fluctuate. Local populations may be radically reduced by long spells of bad weather, as in the New England States (Forbush, 1904), but as shown in this paper, changes of short duration in the weather only affect activity, not overall production. The high productivity of the Edmonton birds has been

sufficient to increase the numbers from probably less than ten pairs in 1946 to an estimated 2000 pairs, 20 years later. Even short spells of "bad" weather, as experienced in 1965, did not greatly alter the population.

Rain of three or more hours duration had the most influence on purple martin activity. The three next most significant weather factors influencing martin ED activity were temperature, sky opacity and wind velocity, with temperature probably being most influential. If the critical 30-day period required for nestling development has a mean temperature above 55°F, martins will probably reproduce successfully. If these conditions are not met colonies may survive for brief stretches of time but permanent colonization will not occur. If wind velocities continually exceed 10 mph during this critical period the adults will have difficulty obtaining sufficient food for the young. Wind in the prairie parkland usually does not blow at such high velocities for long. Of these three weather factors, sky opacity is probably least influential since if the wind is low enough and the temperature high enough to bring insects into the air, martins can feed.

The factor that probably limits the expansion

of the population of purple martins at Edmonton is the availability of nest sites. If additional nest boxes are provided there should be enough aerial insects to support many more martins than are presently produced. Other aerial insect eating animals such as bats are quite successful at raising young in the Edmonton area (J.S. Hayward, pers. comm.). I suspect that competition for nest sites with English sparrows (Passer domesticus) and starlings (Sturnus vulgaris) prevents some of the potential breeding stock from reproducing.

There are several problems raised in this study that remain unanswered. What type of food is brought to nestlings during different ages? Are these flying insects, normally found near the ground? How much food is brought to the young as they become older? Does the amount of food brought by the parents first increase in quantity and then later decrease as the nestlings become older? Is there a change in insect food species brought by the parents both hourly and daily? If so when does this change occur? Are the young in larger broods lighter in weight than small ones? If so, does this weight decrease determine chances of survival of nestlings as reported by Perrins (1965) for tits. What ectoparasites are

most influential on martins, assuming that the numerous external forms found on all nestlings do affect them?

LITERATURE CITED

- Alder, H.L. and E.B. Roessler, 1964. Introduction to probability and statistics. 3rd ed. W.H. Freeman & Co., San Francisco 313 p.
- Allen, R.A., and M.M. Nice. 1952. A study of the breeding biology of the purple martin (Progne subis). Amer. Mid. Nat., 47:606-665.
- Armstrong, E.A. 1955. The wren. Collins, London. 312 p.
- Ayre, G.L. 1958. Some meteorological factors affecting the foraging of Formica subniten Creighton (Hymenoptera: Formicidae). Insectes Sociaux. 5:147-157.
- Bann van der, G. 1954. Varietie in de vogelzang aan de binnenduinrand te schoorl. (Variations in the singing of birds at the eastern part of the dunes at Schoorl, Holland.) Levende Natuur, 57:91-98, 6:113-118.
- Barr, A.R., T.A. Smith and M.M. Boreham. 1960. Light intensity and the attraction of mosquitoes to light traps. J. Econ. Ent., 53:876-880.
- Beal, F.E.L. 1918. Food habits of the swallows, a family of valuable native birds. U.S. Dept. Agr., Bull., 619:1-28.

- Bennett, C.A. and N.L. Franklin. 1954. Statistical analysis in chemistry and the chemical industry. John Wiley and Sons, New York. 724 p.
- Bent, A.C. 1942. Life histories of North American flycatchers, larks, swallows, and their allies. Smithsonian Institute. U.S. Nat. Mus. Bull., 179:489-509.
- Birch, L.C. 1957. The role of weather in determining the distribution and abundance of animals. In p.106-109, E.J. Kormondy, Readings in Ecology. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.
- Brauner, J. 1952. Reactions of poor-wills to light and temperature. Condor, 54:152-159.
- Brewster, W. 1925. The birds of the Lake Umbagog region of Maine. Bull. Mus. Comp. Zool.; Harvard, 66:276-305.
- Bump, G., R.W.Darrow, F.C.Edminster, W.F.Crissey. 1947. The Ruffed Grouse, Life History, Propagation, Management. New York State Conservation Dept., Buffalo, N.Y. 915 p.
- Cloudsley-Thompson, J.L. 1962. Microclimates and the distribution of terrestrial arthropods. Ann. Rev. of Ent., 7:199-222.

- Collins, C.W. and W.L. Baker. 1934. Exploring the upper air for wind-borne gypsy moth larvae. J. Econ. Ent., 27:320-327.
- Davis, D.E. 1963. The role of temperature and light in morning arrival of starlings. Ecology, 44:397-398.
- Dethier, V.G. 1957. The sensory physiology of blood-sucking arthropods. Exp. Parasitol., 6:68-122.
- Edwards, D.K. 1961. Activity of two species of Calliphora (Diptera) during barometric pressure changes of natural magnitude. Can. J. Zool., 39:623-635.
- Elliot, P.R. 1932. Temperature and relative humidity in relation to the ending of the evening song of birds. J. Tenn. Acad. Sci., 7:204-213.
- Forbush, E.H. 1904. The destruction of birds by the elements in 1903-04. Ann. Rept. Mass. State Bd. Agr., 51:457-503.
- _____. 1929. Birds of Massachusetts and other New England states. Mass. Dept. Agri., Boston, 466 p.

- Freeman, J.A. 1945. Study in the distribution of insects by aerial currents. J. Animal Ecol., 14:128-154.
- Gaunt, A.S. 1959. Behaviour in the purple martin. Kansas Ornith. Soc. Bull., 10:14-16.
- Gibb, J. 1955. Feeding rates of great tits. Br. Birds, 48:49-58.
- Glick, P.A. 1939. The distribution of insects, spiders and mites in the air. U.S. Dept. Agr. Tech. Bull., 673:1-150.
- _____ 1942. Insect populations and migration in the air. Aero Biology, Am. Ass. Advancement Sci., Wash., 17:88-98.
- _____ 1955. Pink bollworm moth collections in airplane traps. J. Econ. Ent., 48:767.
- _____ 1957. Collecting insects by airplane in southern Texas. U.S. Dept. Agr. Tech. Bull. 1158. 22 p.
- Glick, P.A. and L.W. Noble. 1961. Airborne movement of the pink bollworm and other arthropods. U.S. Dept. Agr. Tech. Bull. 1255:1-20.
- Groebbels, F. 1956. Untersuchung uber den morgendlichen Beginn und die abendliche Beendigung der Stimmausserungen von Vogelarten.

Ornith. Mitt., 8:61-66.

Hardy, A.C. and P.S. Milne. 1938. Studies in the distribution of insects by aerial currents. Experiments in aerial tow netting from kites. J. Anim. Ecol., 7:199-229.

Jacobs, J.W. 1903. The story of a martin colony. Gleanings, 2:1-24.

Johnston, R.F. 1967. Seasonal variation in the food of the purple martin Progne subis in Kansas. Ibis, 109:8-13.

Johnston, R.F. and J.W. Hardy. 1962. Behaviour of the purple martin. Wilson Bull., 74:243-262.

Jones, L. 1917. The May migration 1917 at Oberlin, Ohio. Wilson Bull., 29:103-104.

Kendeigh, S.C. 1952. Parental care and its evolution in birds. U. of Ill. Press, Urbana. 358 p.

Koskimies, J. 1950. The life of the swift, Micropus apus. (L.) in relation to the weather. Ann. Acad. Sci. Fenn., 1-151.

Kuroda, N. 1964. The comparative analysis of breeding rates of rural and urban grey starling colonies in Tokyo area II. Misc. Rep. Yamashina's Inst. Ornitol. Zool., 4:1-30.

- Lack, D. 1947. The Significance of Clutch size.
Ibis, 89:302-352.
- _____ 1948. Natural selection and family size
in starlings. Evolution, 2:95-110.
- _____ 1954. The natural regulation of animal
numbers. Clarendon, Oxford. 343 p.
- Lack, D. and E. Lack. 1951. The breeding biology
of the swift Apus apus. Ibis,
93:501-546.
- Lee, J.A. 1967. Relative reproductive efficiency
of adult and sub-adult purple martins.
Chat, 31:1-2.
- Leopold, A. and A.E.Eyon. 1961. Avian daybreak
and evening song in relation to time
and light intensity. Condor, 63:269-293.
- Lewis, J.B. 1950. The effect of weather upon
insect populations. Unpublished M.Sc.
thesis, McGill Univ. 116 p.
- List, R.J. 1951. Smithsonian Meteorological Tables.
Pub. 4014, 6th Edition, Vol.114. 527 p.
- MacArthur, R.H. 1961. Population effects of natural
selection. Amer. Nat., 95:195-199.
- Maslov, A.V. 1964. Conditions of life and the
normal behaviour of the larvae of the
mosquito Culiseta bergrothi (Diptera
Culcidae). Zool. Zh., 43:859-871.

- McClure, H.E. 1938. Insect aerial populations.
Ann. Ent. Soc. Amer., 31:504-513.
- McConnell, T.L. 1918. High mortality among purple martins in Western Pennsylvania during April, 1917. Bird Lore, 20:130-131.
- Meyer, M.T. 1957. Clutch size and laying dates in cliff swallow colonies. Condor, 59:311-316.
- Minar, J. 1962. The influence of meteorological factors on the activity of some parasitic Diptera (Ceratopogonidae, Simuliidae, Tabanidae). Ceskoslov. Parasitol., 9:331-342.
- Moreau, R.E. 1939. Numerical data on African birds' behaviour at the nest Hirundo s. smithii Leach, the wire tailed swallow. Proc. Zool. Soc. London, A, 109:109-125.
- _____ 1940. Numerical data on African birds' behaviour at the nest II. Psolidoprocne holomelaena massaica Neum., the rough-wing bank martin. Ibis, 14:234-248.
- _____ 1947. Relations between number in brood, feeding rate and nestling period in nine species of birds in Tanganyika Territory. J. Anim. Ecol., 16:205-209.

- Morley A. 1943. Sexual behaviour in British birds from October to January. *Ibis*, 85:132-158.
- Nice, M. M. 1937. Studies in the life history of the song sparrow. I. Dover Publications 1964 reprint, New York. 246 p.
- _____ 1943. Studies in the life history of the sparrow. II. Dover Publications 1964 reprint, New York. 328 p.
- Nice, M.M. and R.H. Thomas. 1948. A nesting of the Carolina Wren. *Wilson Bull.*, 60:139-158.
- Nicholson, A.J. 1957. The self-adjustment of populations to change. Cold Spring Harbor Symposium Quantitative Biol., 22:153-172.
- Olmstead, R. 1955. Observations on purple martins. *Bull. Kansas Ornith. Soc.*, 6:8-10.
- Palmgren, P. 1935. Uber den Tagesrhythmus der vogel im arktischen sommer. *Ornis Fenn.* 12:107-121.
- _____ 1949. On the diurnal rhythm of activity and rest in birds. *Ibis*, 91:561-575.
- Paynter, R.A. 1954. Interrelations between clutch-size, brood-size, pre-fledging survival, and weight in Kent Island tree swallows. Pt. I, II, III. *Bird Banding*, 25:35-58, 102-110, 136-148.

- Perrins, C.M. 1965. Population fluctuations and clutch-size in the great tit, Parus major L. J. Anim. Ecol., 34:601-647.
- Peterson, A.J. 1955. The breeding cycle in the bank swallow. Wilson Bull., 67:235-286.
- Peterson, R.T. 1961. A field guide to western birds. Houghton Mifflin Co., Boston. 366 p.
- Pettingill, O.S. Jr. 1961. A laboratory and field manual of ornithology. Burgess Publishing Co., Minneapolis. 381 p.
- Pinchin, R.D. and J. Anderson. 1936. On the nocturnal activity of Tipulinae (Dipterae) as measured by a light trap. (2) The influence of temperature, cloud and moonlight on the numbers of insects captured. Proc. R. Ent. Soc. London A, 11:75-78.
- Prince, R.P., J.H. Whitaker, L.D. Matterson and R.E. Luginbuhl. 1965. Response of chickens to temperature and relative humidity environments. Poultry Sci., 44:73-77.
- Purchon, R.D. 1948. The nesting activity of the swallow. Proc. Zool. Soc. London, 118:146-170.

- Royama T. 1966. Factors governing feeding rate, food requirements and brood size of nestling great tits Parus major. Ibis, 108:313-347.
- Scheer, G. 1952. Observations and investigations on the internal and external factors upon which early morning singing depends. D.Sc. thesis. Tech. Hochschule Darmstadt. 114 p. Biol. Ab. 3/4:1-68.
- Schoennagel, E. 1963. The dependence of the evening feeding flights on mallards on light intensity. Proc. Internatl. Ornithol. Congr., 13:293-298.
- Skutch, A. 1962. The constancy of incubation. Wilson Bull., 74:115-152.
- Southern, W.E. 1959. Homing of purple martins. Wilson Bull., 71:254-261.
- Taylor, L.R. 1963. Analysis of the effect of temperature on insects in flight. J. Anim. Ecol., 32:99-117.
- Thomson, Sir A. L. 1964. New Dictionary of Birds. Thomas Nelson. London. 928 p.
- Verner, J. 1965. Breeding biology of the long-billed marsh wren. Condor, 67:6-30.

- Weise, C.M. 1956. Nightly unrest in caged migratory sparrows under outdoor conditions. *Ecology*, 37:274-287.
- Wellington, W.G. 1945. Conditions governing the distribution of insects in the free atmosphere. *Can. Ent.*, 77:7-17, 21-28, 44-49, 69-74.
- Welty, J.C. 1962. The life of birds. W.B. Saunders Co., Philadelphia. 546 p.
- Widmann, O. 1922. Extracts from the diary of Otto Widmann. *Trans. Acad. Sci. St. Louis*, 24:1-77.
- Williams, C.B. 1961. Studies in the effect of weather conditions on the activity and abundance of insect populations. *Phil. Trans. Roy. Soc., Ser. B. Biol. Sci.*, 244:331-378.
- Williams, L. 1941. Roosting habits of the chestnut-backed chickadee and the winter wren roost. *Condor*, 43:274-285.
- Willson, M.F. 1966. Breeding ecology of the yellow-headed blackbird. *Ecol. Monographs*. 36:51-77.

Appendix I. Nest boxes used in 1965 to collect data on purple martin activity at the nest entrance. The upper photo was taken in mid-July during the nestling stage while the lower photo was taken in early August when most birds were participating in post-breeding defence of nest entrances.

Photos: A. Porcher.



Appendix II.

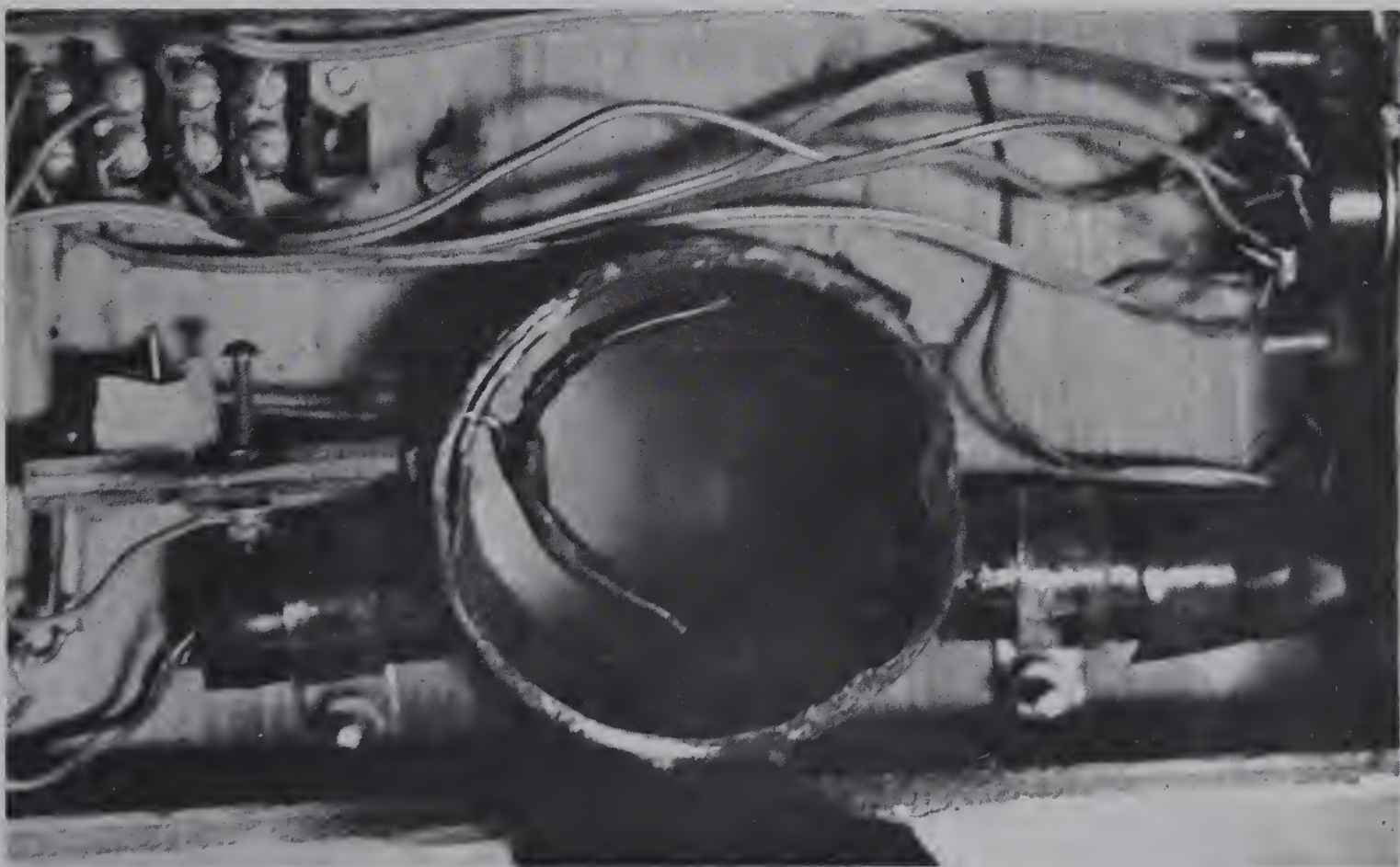
Three of the four purple martin nest complexes used in 1966 at Elk Island National Park. The two colonies on the right each contained six experimental nests and three controls. The colony on the left was used as a control and contained six nests to which dummy units were attached similar to the photocell ones but lacking both wiring and light sources. The three central boxes were left without attached units as in the other two apartments.

Photo: A. Karvonen



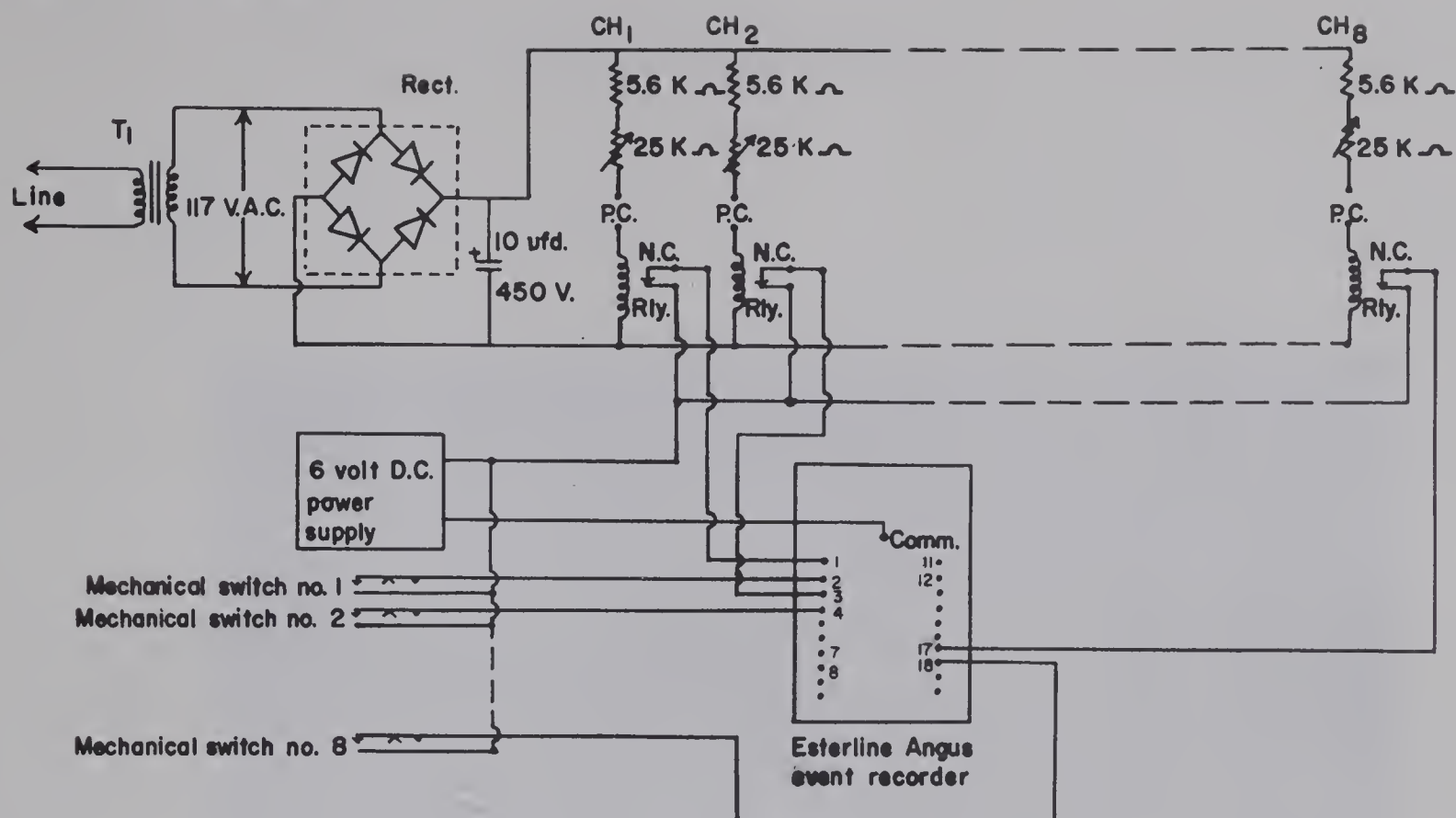
Appendix III. One of the photo electric and mechanical switch unit boxes which were attached to each nest box to record the number of nest entrances and departures by purple martins in 1965.

The upper photo illustrates the unit closed and in place. The mechanical switch can be seen at the left in the entrance. The lower photo illustrates the contents of the unit. The photo-cell is at the left bottom, the light source at the lower right and the mechanical switch overlies the photo-cell on the left.

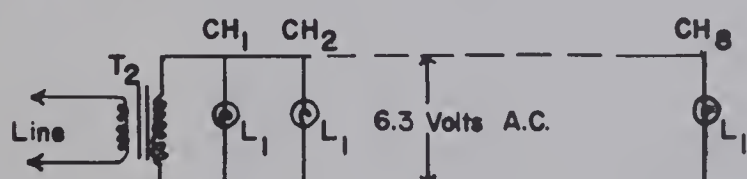


Appendix IV. Circuit diagram of the 1965 and 1966 electronic setup used for measuring the number of nest entrances and departures by purple martins in the Edmonton region.

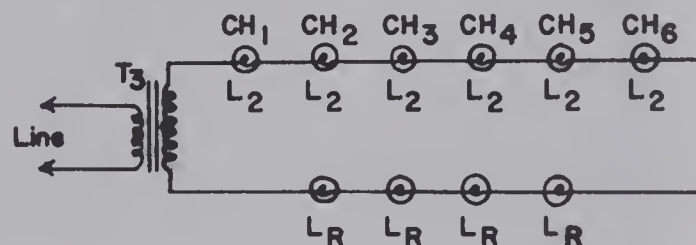
1965 CIRCUIT DIAGRAM



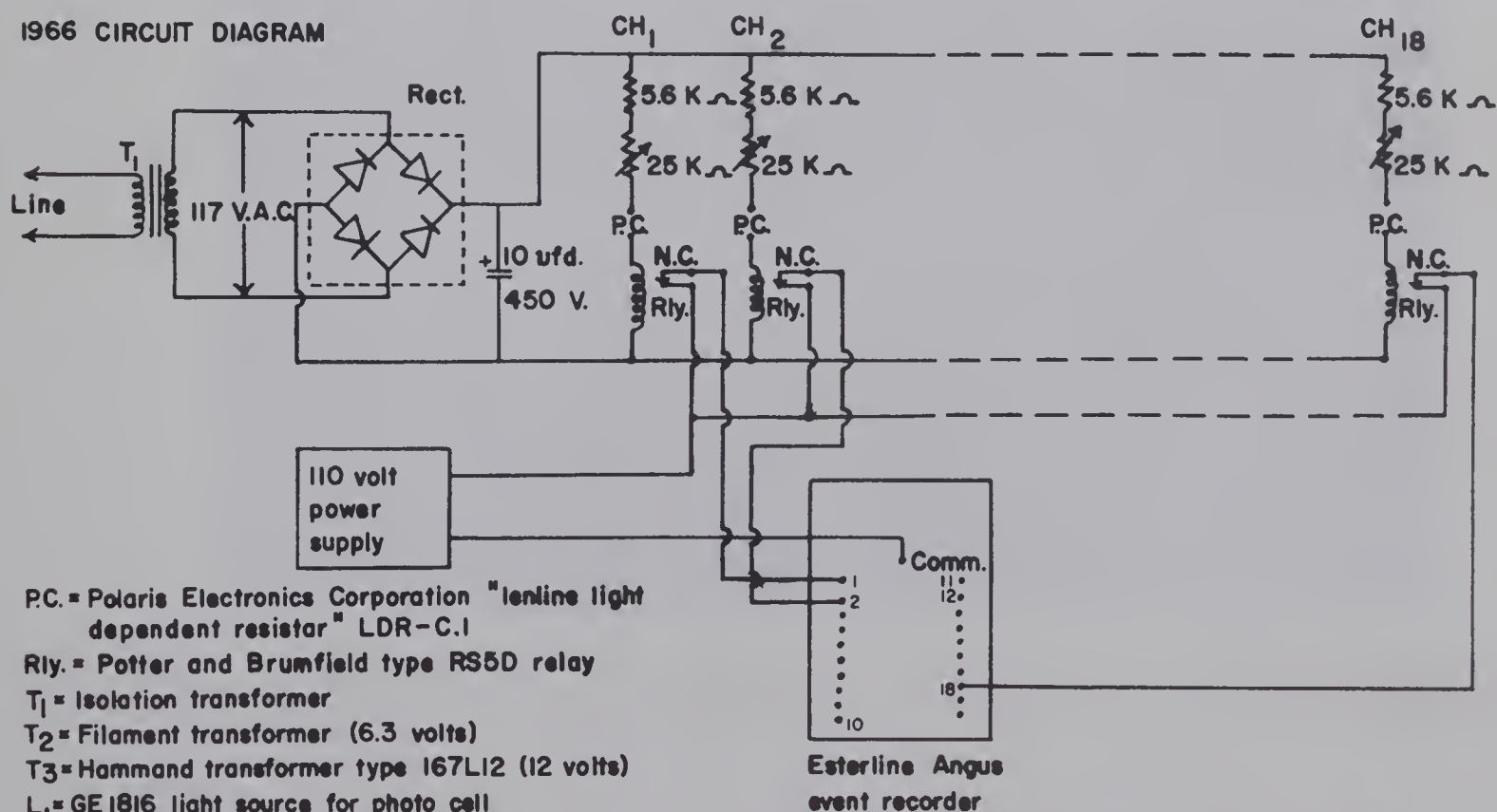
1965 LIGHT SOURCE



1966 LIGHT SOURCE



1966 CIRCUIT DIAGRAM



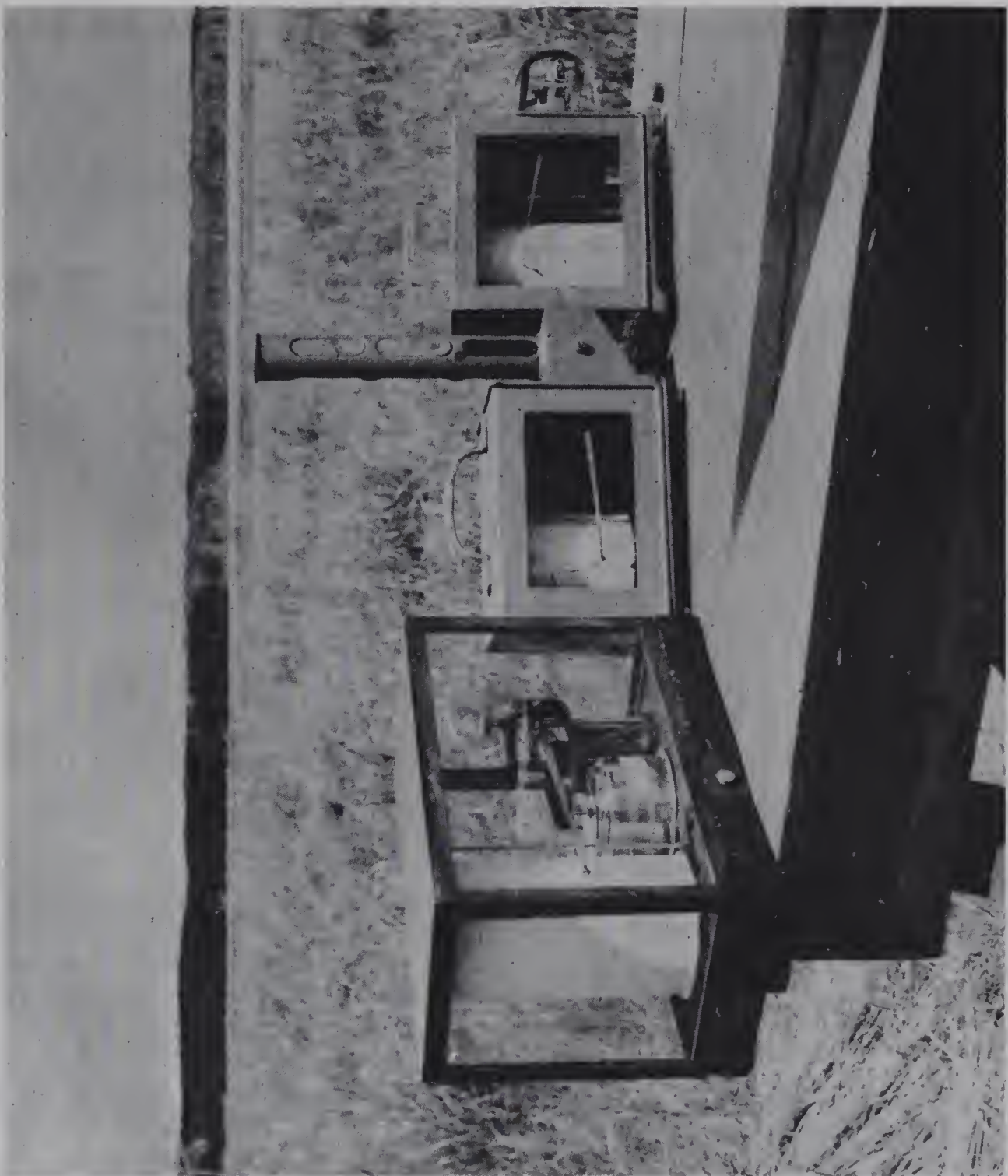
P.C. = Polaris Electronics Corporation "lenline light dependent resistor" LDR-C.1
 Rly. = Potter and Brumfield type RS5D relay
 T₁ = Isolation transformer
 T₂ = Filament transformer (6.3 volts)
 T₃ = Hammand transformer type 167L12 (12 volts)
 L₁ = GE 1816 light source for photo cell
 L₂ = GE 222 light source for photo cell
 L_R = GE 222 light used as resistor
 Comm. = Common
 Rect. = General Electric type BH4R4 bridge rectifier

V.A.C. = Volts Alternating Current
 N.C. = Normally Closed
 ufd. = Micro farrad
 C.H. = Channel

K Ω = Kilo/ohm
 V. = Volts
 A.C. = Alternating Current
 D.C. = Direct Current

Appendix V. Meteorological instruments used to collect data at Elk Island National Park in 1966. The instruments are from right to left: thermograph, hygrogograph and a barograph. Protective housing was removed before photograph was taken.

Photo: A. Karvonen

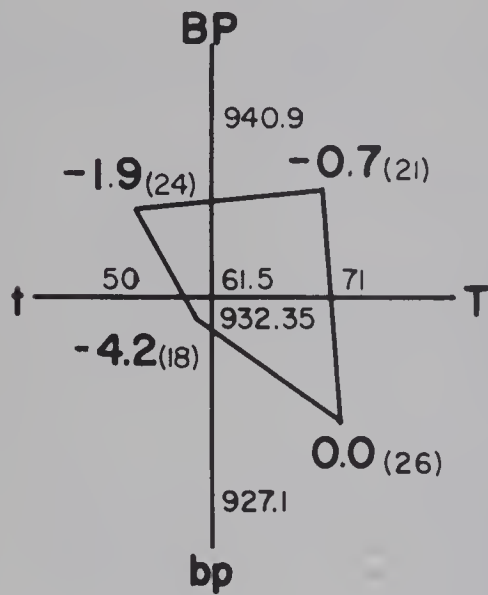


Appendix VI. Purple martin activity at the nest entrance during the nestling period as influenced by two meteorological factors in combination: in each figure one factor, barometric pressure, is combined with one factor including temperature, sky opacity, wind velocity and relative humidity.

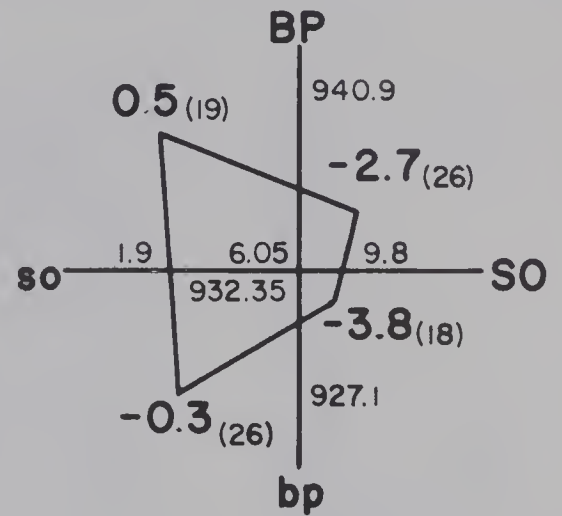
Numbers in bold type represent the mean of the differences from the "ideal" feeding curve (as discussed in the text) under prevailing meteorological conditions in specific quadrants of the graph. They also represent the distance in arbitrary units from the origin along a line at 45° to the major axes. They form the corners of the polygons. Numbers in fine type indicate the median and range of values on the X and Y axes. Numbers in fine type and bracketed indicated sample size (number of pairs).

NESTLING STAGE

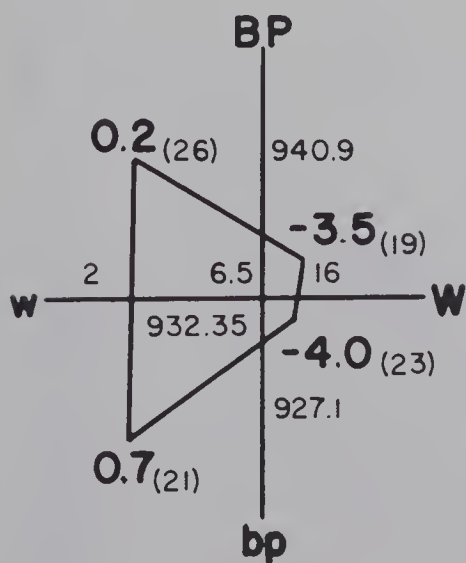
TEMPERATURE vs.
BAROMETRIC PRESSURE



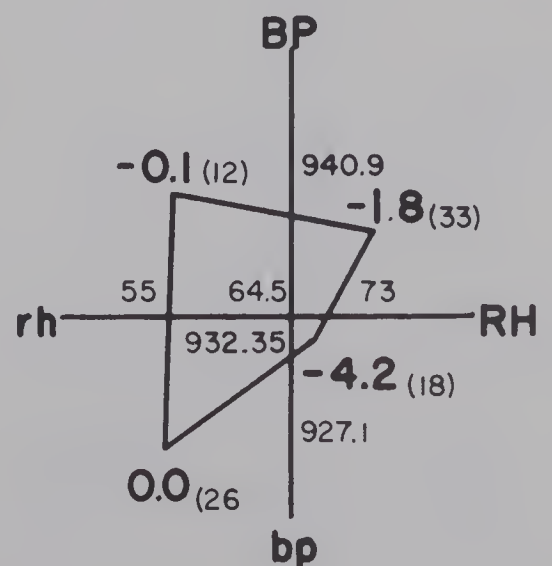
SKY OPACITY vs.
BAROMETRIC PRESSURE



WIND vs.
BAROMETRIC PRESSURE



RELATIVE HUMIDITY vs.
BAROMETRIC PRESSURE



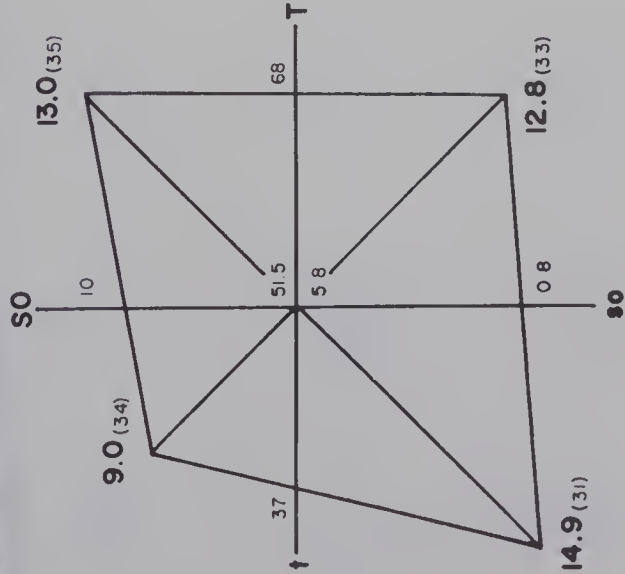
Appendix VII.

Purple martin activity at the nest entrance as influenced by the two factors: temperature and sky opacity.

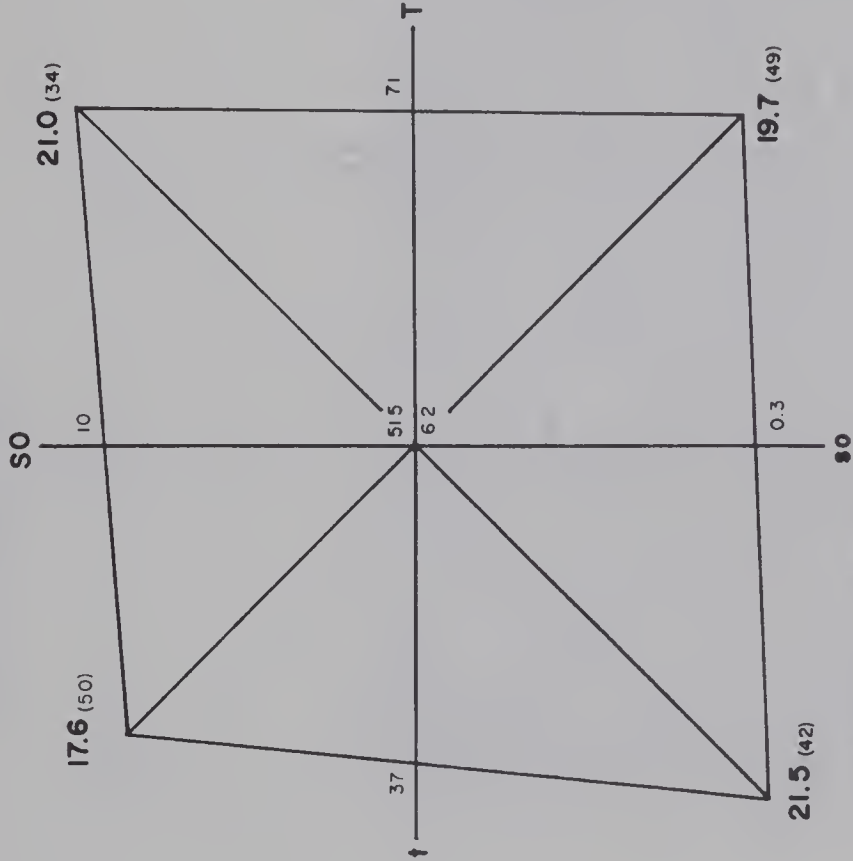
Numbers in bold type indicate the mean number of nest entrance activity values (except for the nestling stage in which instance these numbers represent the mean of the differences from the "ideal" feeding curve as discussed in the text) under prevailing meteorological conditions in specific quadrants of the graph. They also represent the distance in arbitrary units from the origin along a line at 45° to the major axis. They form the corners of the polygons. Numbers in fine type indicate the median and range of values on the X and Y axes. Numbers in fine type and bracketed indicate sample size (number of pairs).

TEMPERATURE vs. SKY OPACITY

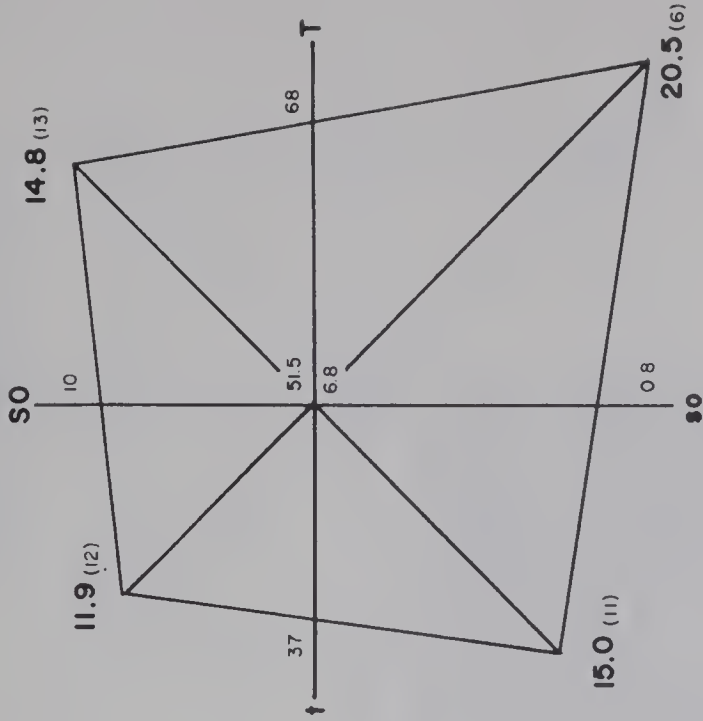
ARRIVAL, NEST DEFENCE, and PAIR-BOND FORMATION STAGE



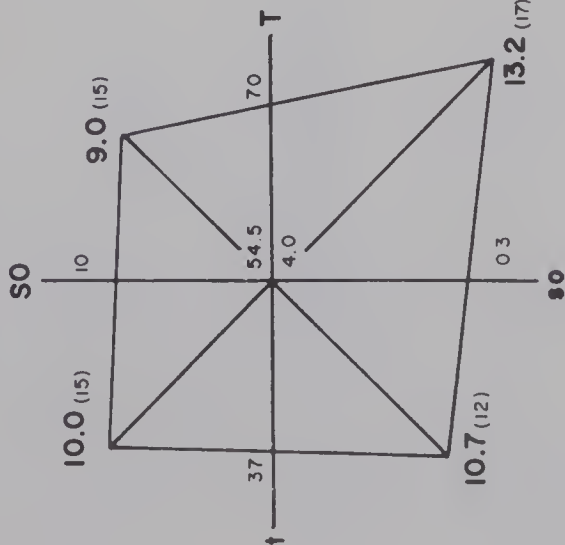
NEST BUILDING STAGE



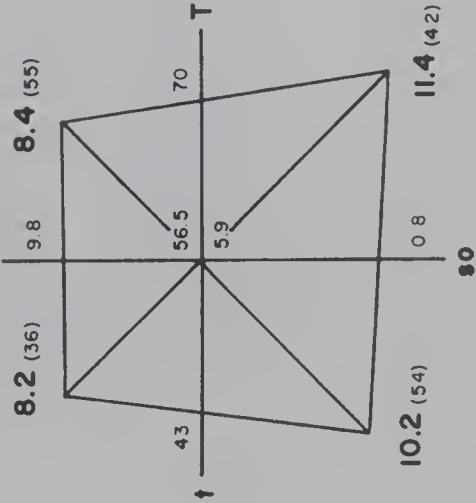
NEST COMPLETION STAGE



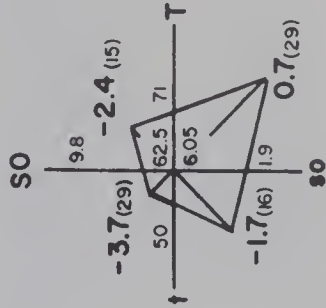
LAYING STAGE



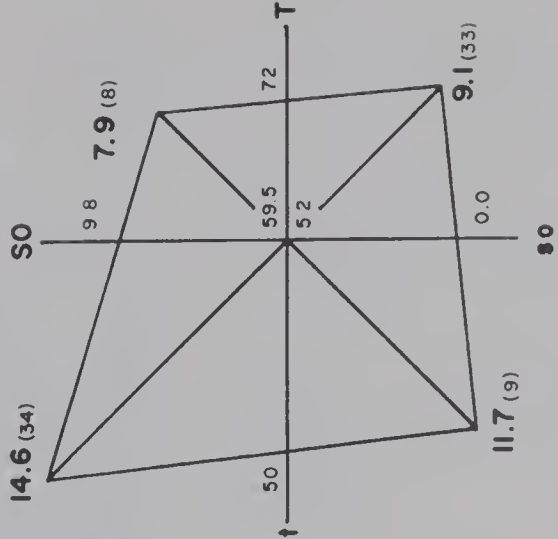
INCUBATION STAGE



NESTLING STAGE



POST-BREEDING STAGE

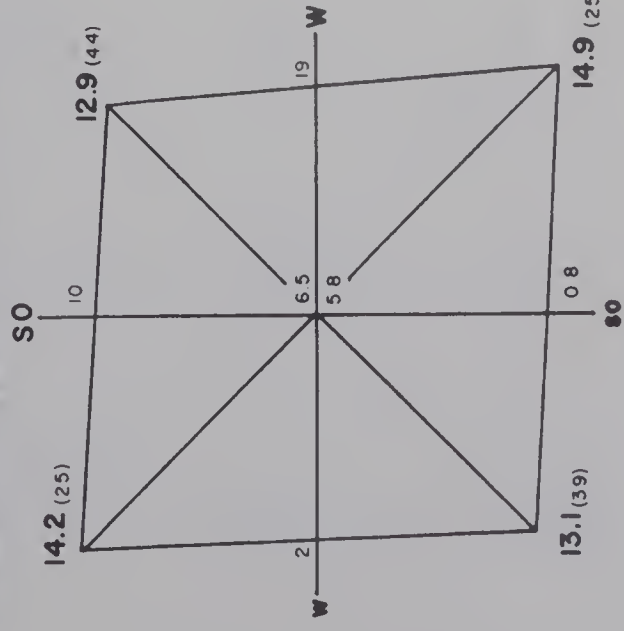


purple martin activity at the nest entrance as influenced by the two factors: wind velocity and sky opacity.

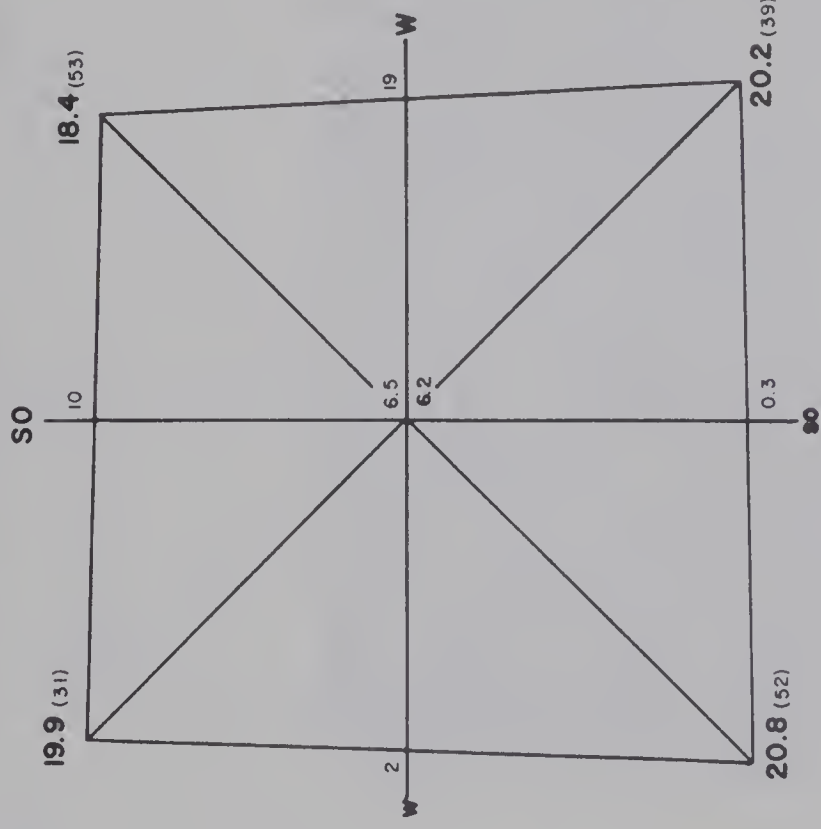
Numbers in bold type indicate the mean number of nest entrance activity values (except for the nestling stage in which instance these numbers represent the mean of the differences from the "ideal" feeding curve as discussed in the text) under prevailing meteorological conditions in specific quadrants of the graph. They also represent the distance in arbitrary units from the origin along a line at 45° to the major axes. They form the corners of the polygons. Numbers in fine type indicate the median and range of values on the X and Y axes. They form the corners of the polygons. Numbers in fine type and bracketed indicate sample size (number of pairs).

WIND vs. SKY OPACITY

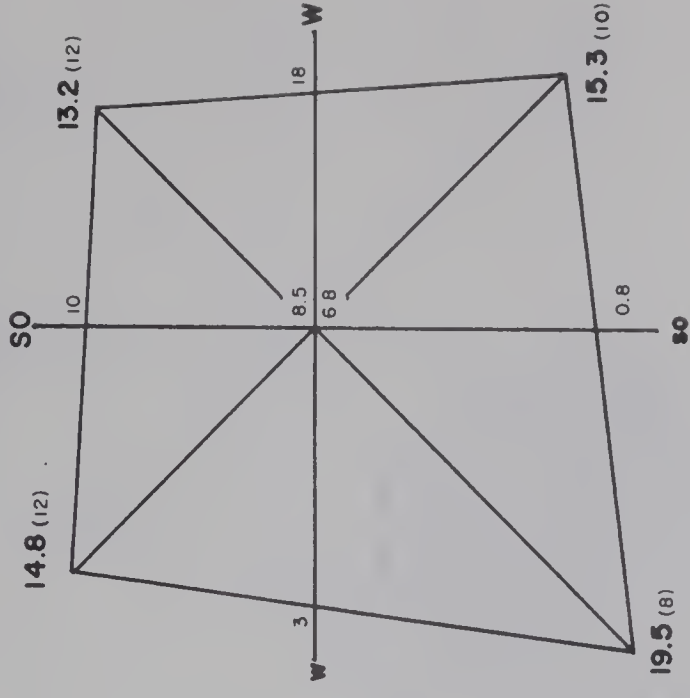
ARRIVAL, NEST DEFENCE, and PAIR-BOND
FORMATION STAGE



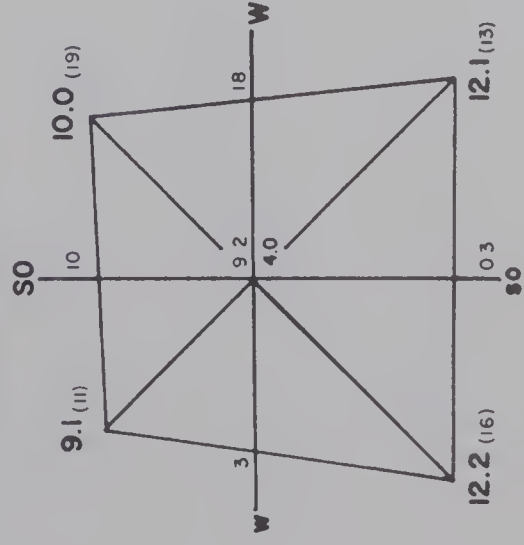
NEST BUILDING STAGE



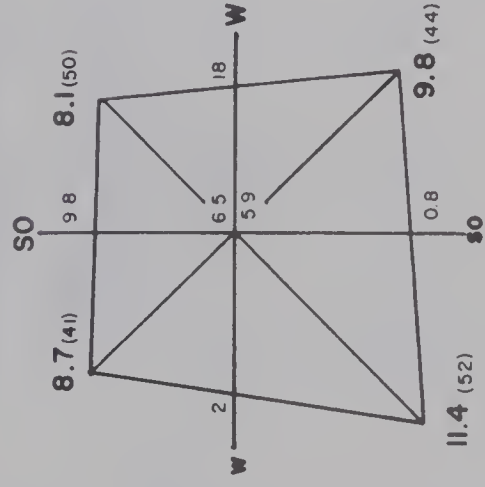
NEST COMPLETION STAGE



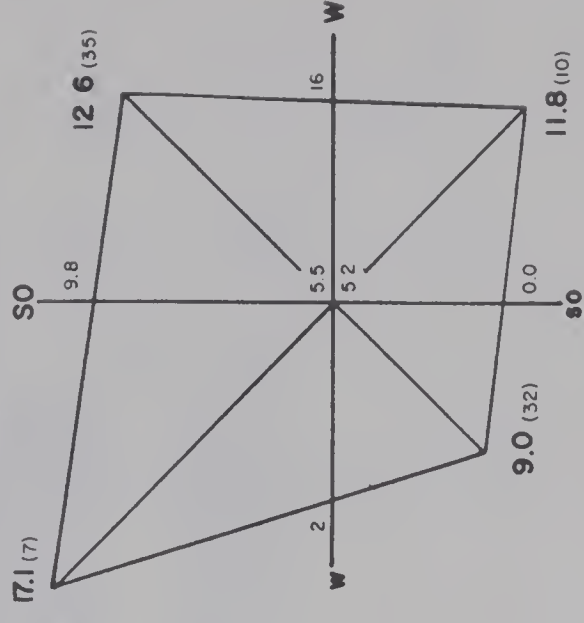
LAYING STAGE



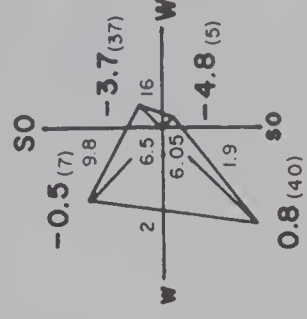
INCUBATION STAGE



POST-BREEDING STAGE



NESTLING STAGE



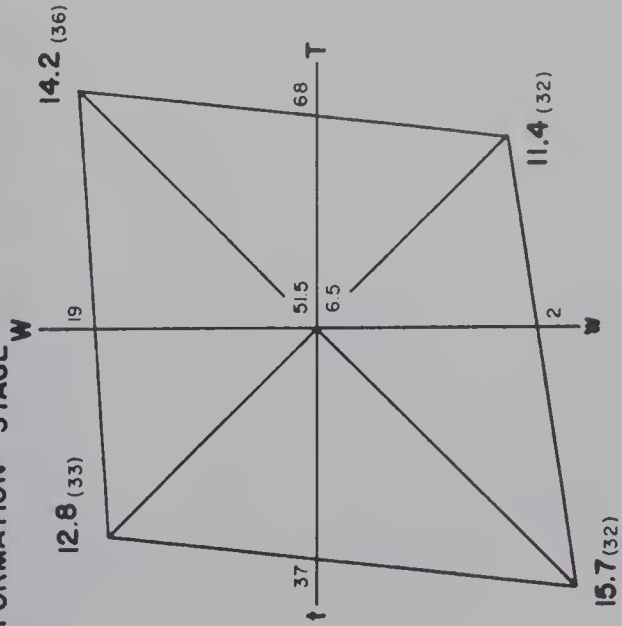
Appendix IX.

Purple martin activity at the nest entrance as influenced by the two factors: temperature and wind velocity.

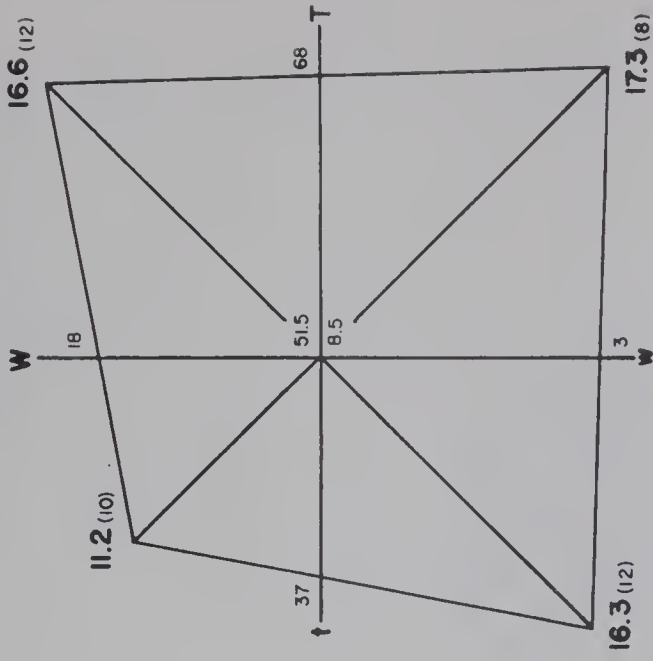
Numbers in bold type indicate the mean number of nest entrance activity values (except for the nestling stage in which instances these numbers represent the mean of the differences from the "ideal" feeding curve as discussed in the text) under prevailing meteorological conditions in specific quadrants of the graph. They also represent the distance in arbitrary units from the origin along a line at 45° to the major axes. They form the corners of the polygons. Numbers in fine type indicate the median and range in values on the X and Y axes. Numbers in fine type and bracketed indicate sample size (number of pairs).

TEMPERATURE vs. WIND

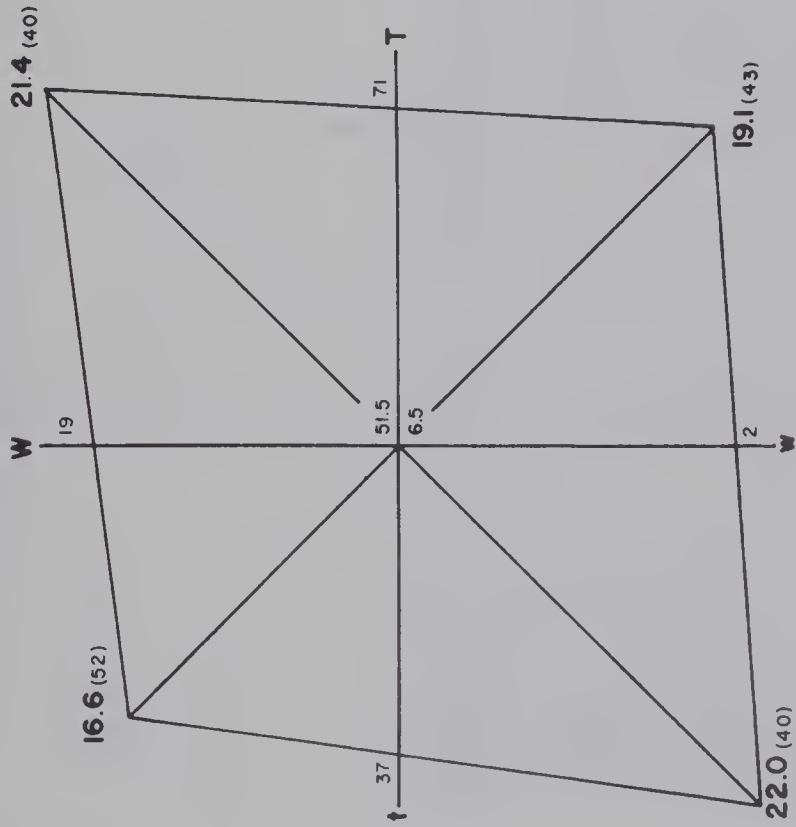
ARRIVAL, NEST DEFENCE, and PAIR-BOND FORMATION STAGE



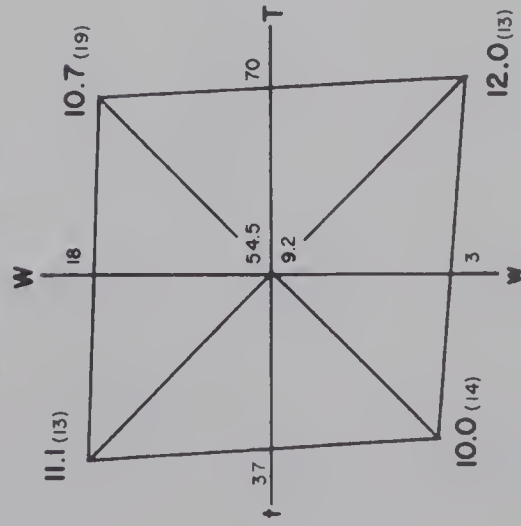
NEST COMPLETION STAGE



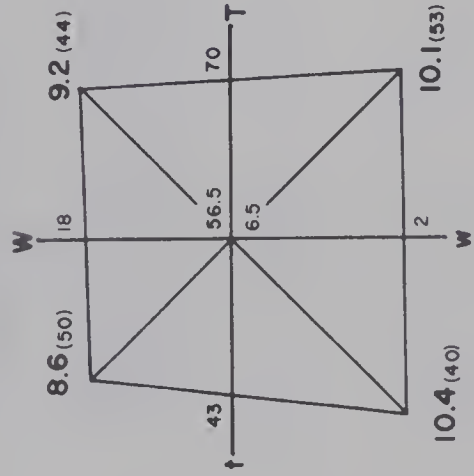
NEST BUILDING STAGE



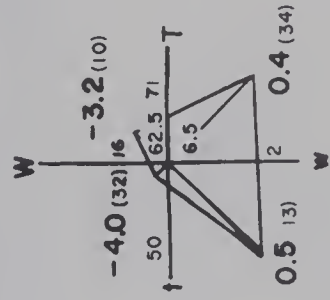
LAYING STAGE



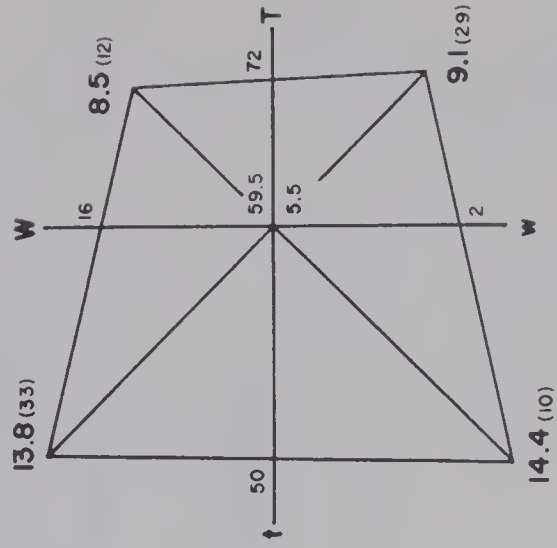
INCUBATION STAGE



NESTLING STAGE



POST-BREEDING STAGE



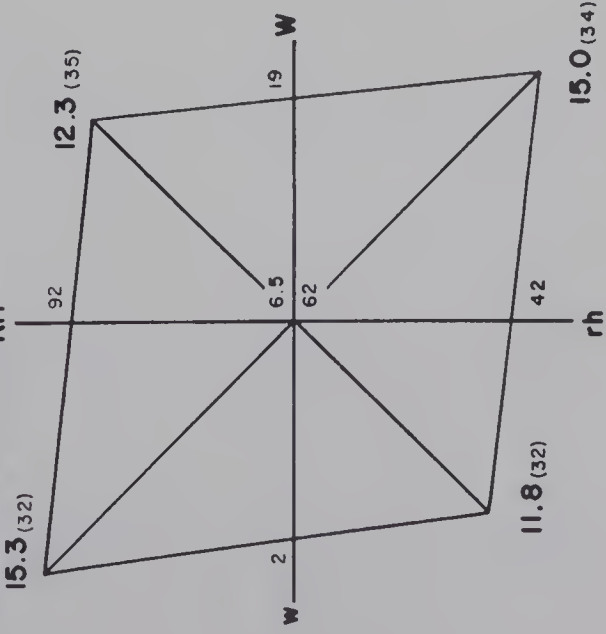
Appendix X.

Purple martin activity at the nest entrance as influenced by the two factors: wind velocity and relative humidity.

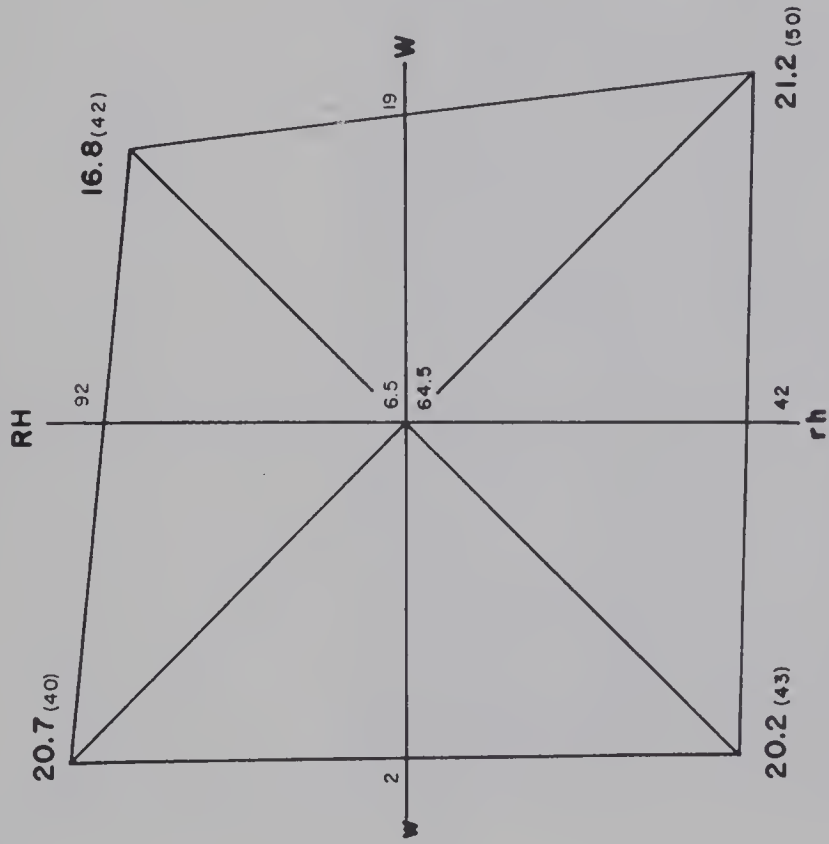
Numbers in bold type indicate the mean number of nest entrance activity values (except for the nestling stage when these numbers represent the mean of the differences from the "ideal" feeding curve as discussed in the text) under prevailing meteorological conditions in specific quadrants of the graph. They also represent the distance in arbitrary units from the origin along a line at 45° to the major axes. They form the corners of the polygons. Numbers in fine type indicate the median and range values on the X and Y axes. Numbers in fine type and bracketed indicate sample size (number of pairs).

WIND vs. RELATIVE HUMIDITY

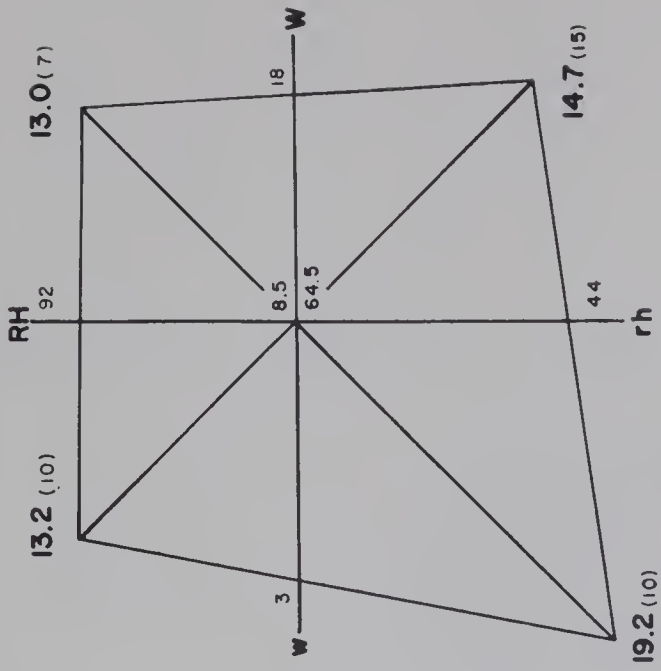
ARRIVAL, NEST DEFENCE, and PAIR-BOND
FORMATION STAGE RH



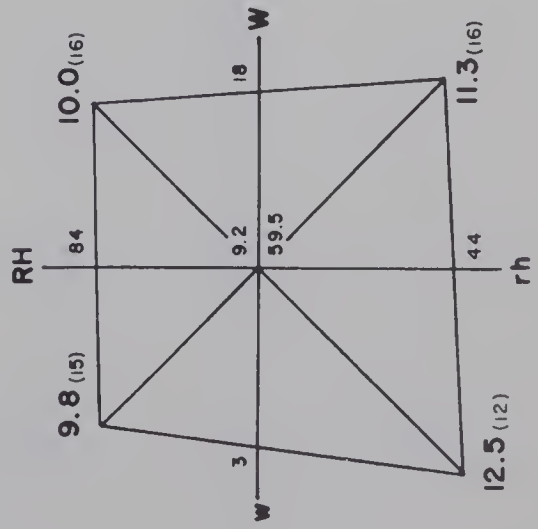
NEST BUILDING STAGE



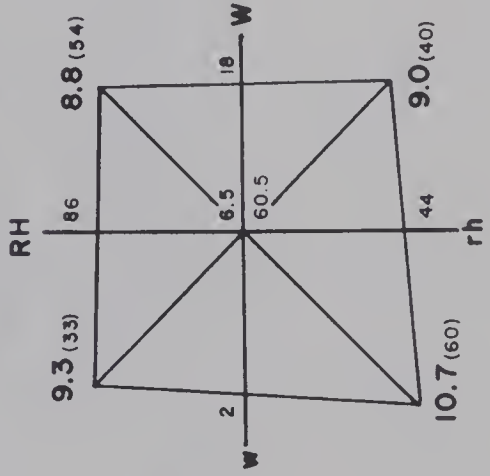
NEST COMPLETION STAGE



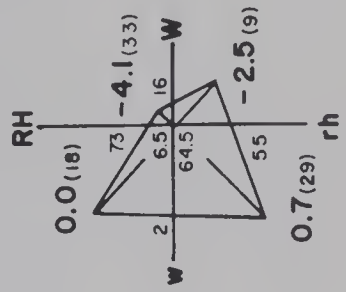
LAYING STAGE



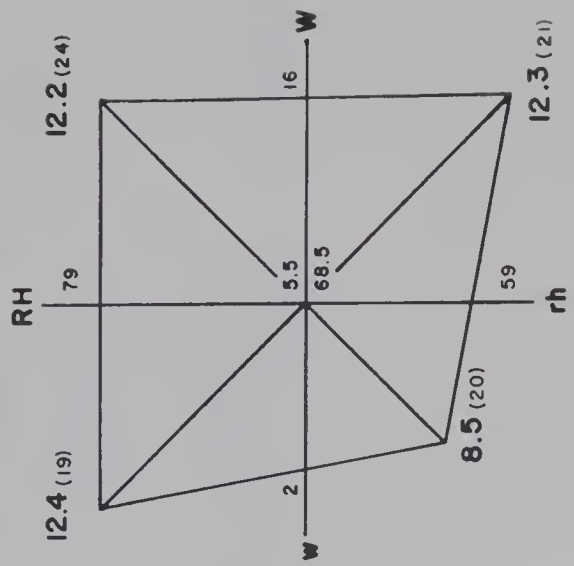
INCUBATION STAGE



NESTLING STAGE



POST-BREEDING STAGE

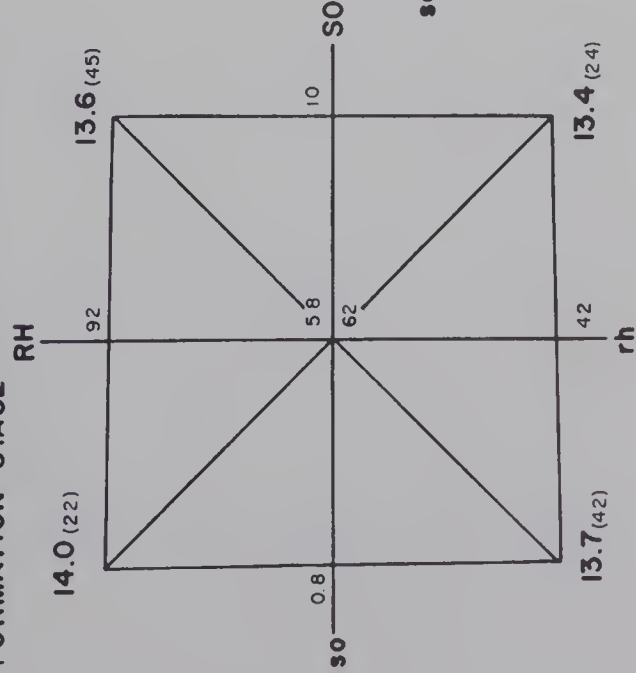


Purple martin activity at the nest entrance as influenced by the two factors: sky opacity and relative humidity.

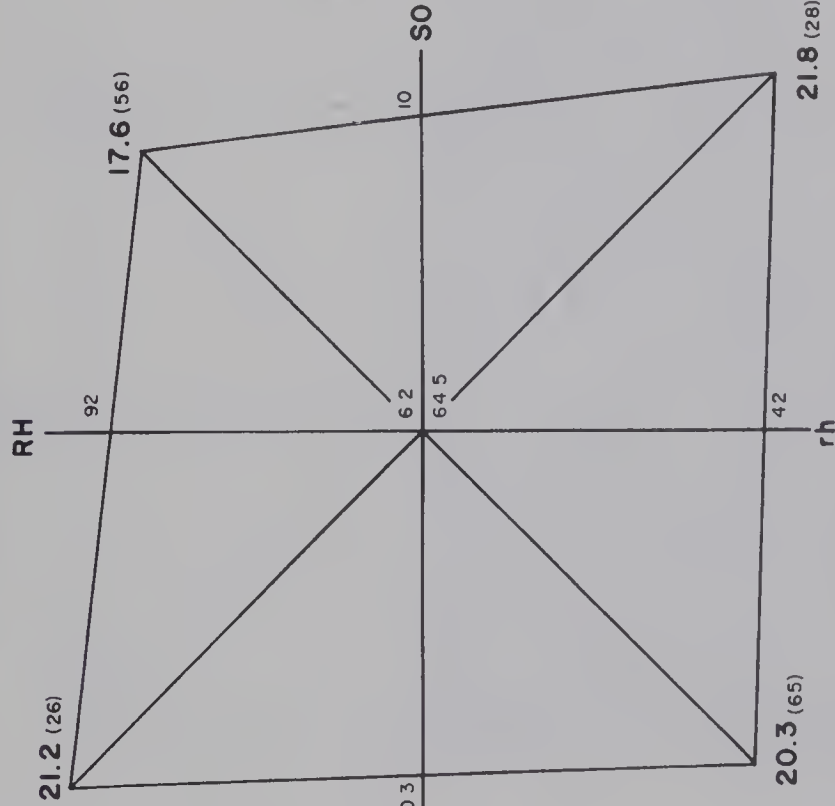
Numbers in bold type indicate the mean number of nest entrance activity values (except for the nestling stage when these numbers represent the mean of the differences from the "ideal" feeding curve as discussed in the text) under prevailing meteorological conditions in specific quadrants of the graph. They also represent the distance in arbitrary units from the origin along a line at 45° to the major axes. They form the corners of the polygons. Numbers in fine type indicate the median and range of values on the X and Y axes. Numbers in fine type and bracketed indicate sample size (number of pairs).

SKY OPACITY vs. RELATIVE HUMIDITY

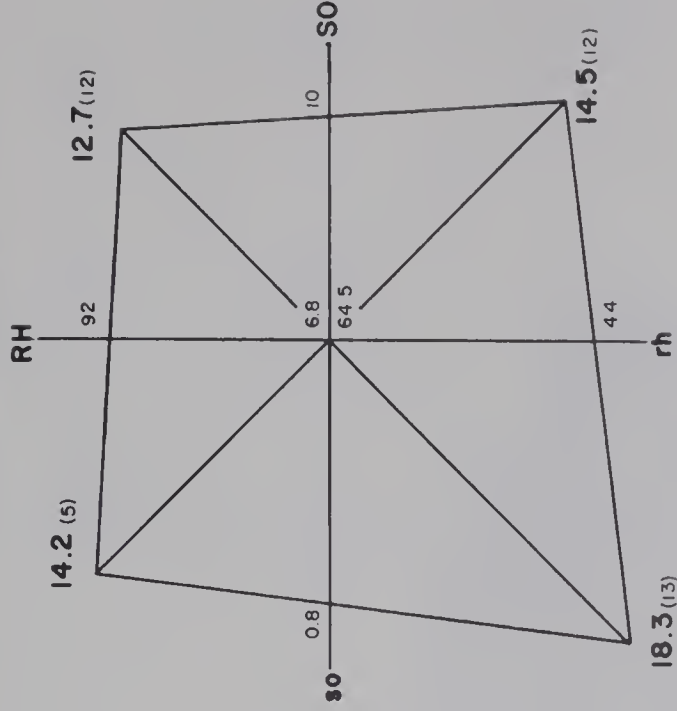
ARRIVAL, NEST DEFENCE, and PAIR-BOND FORMATION STAGE



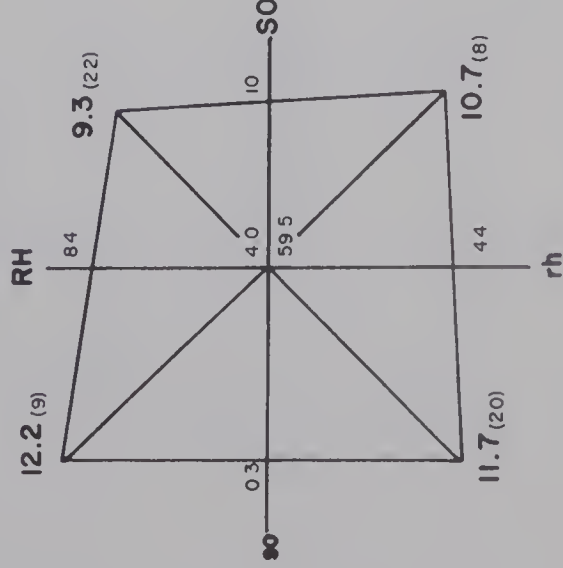
NEST BUILDING STAGE



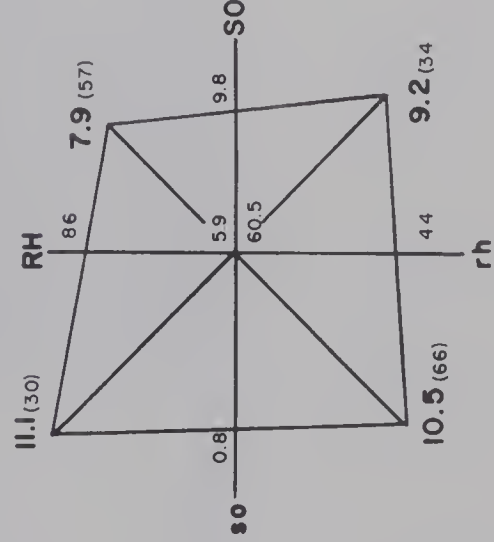
NEST COMPLETION STAGE



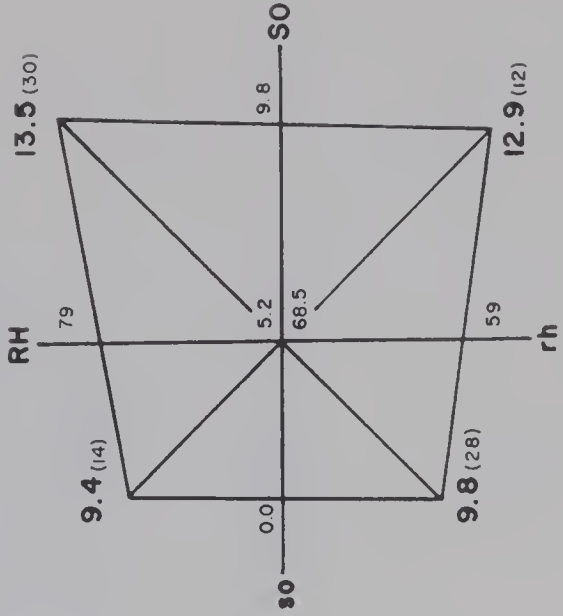
LAYING STAGE



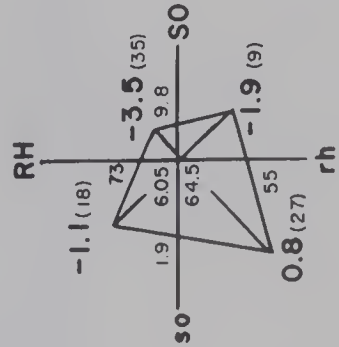
INCUBATION STAGE



POST-BREEDING STAGE



NESTLING STAGE

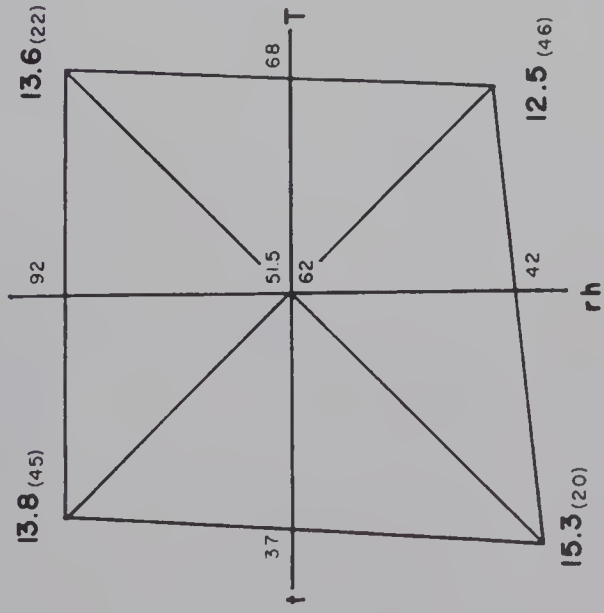


Purple martin activity at the nest entrance as influenced by the two factors: temperature and relative humidity.

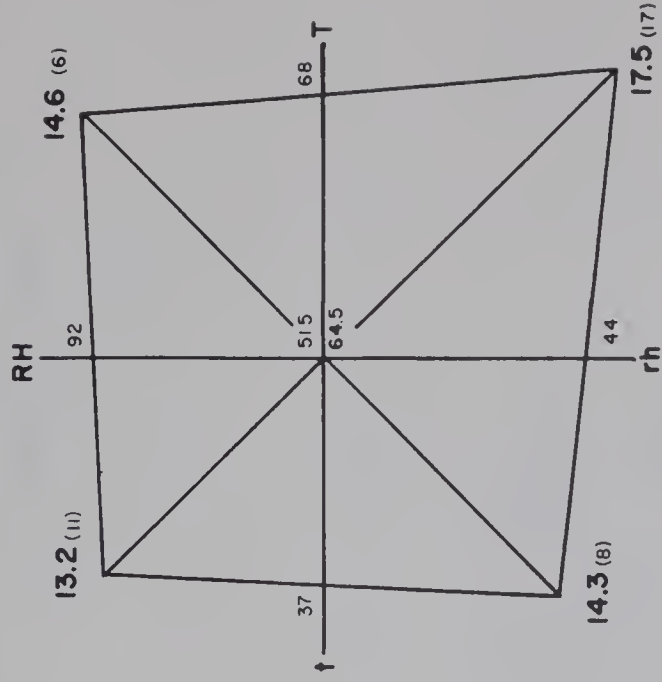
Numbers in bold type indicate the mean number of nest entrance activity values (except for the nestling stage when these numbers represent the mean of the differences from the "ideal" feeding curve as discussed in the text) under prevailing meteorological conditions in specific quadrants of the graph. They also represent the distance in arbitrary units from the origin along a line at 45° to the major axes. They form the corners of the polygons. Numbers in fine type indicate the median and range of values on the X and Y axes. Numbers in fine type and bracketed indicate sample size (number of pairs).

TEMPERATURE vs. RELATIVE HUMIDITY

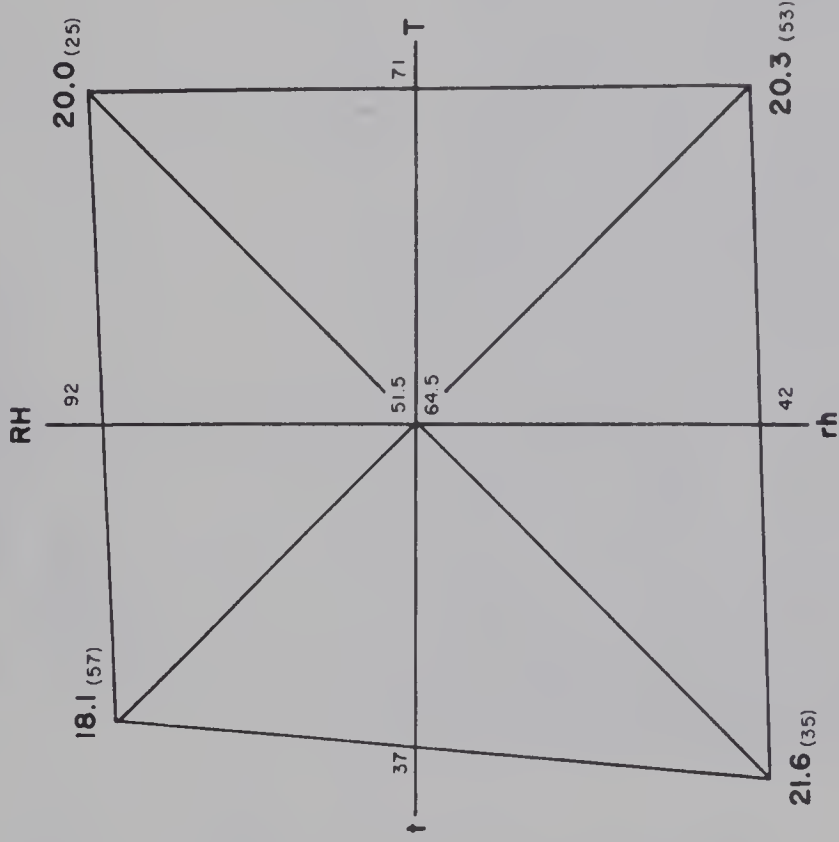
ARRIVAL, NEST DEFENCE and PAIR-BOND FORMATION STAGE RH



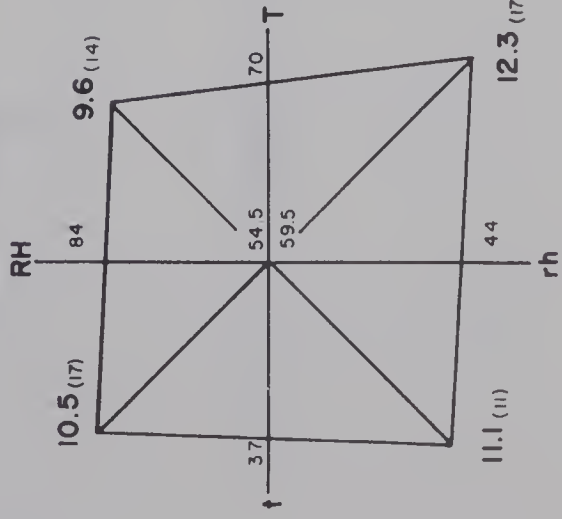
NEST COMPLETION STAGE



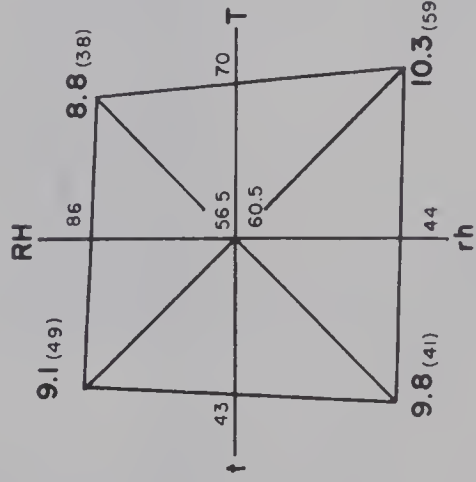
NEST BUILDING STAGE



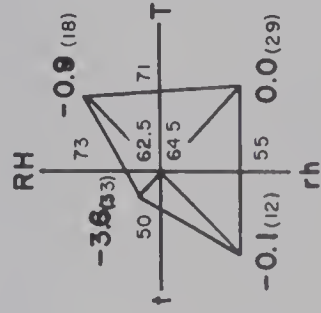
LAYING STAGE



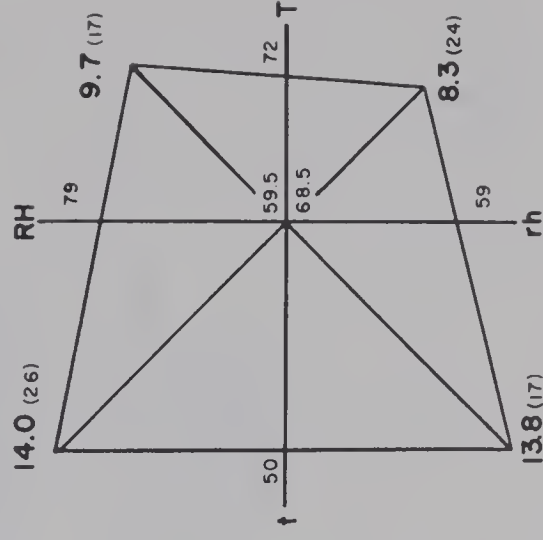
INCUBATION STAGE



NESTLING STAGE



POST-BREEDING STAGE



Appendix XIII.

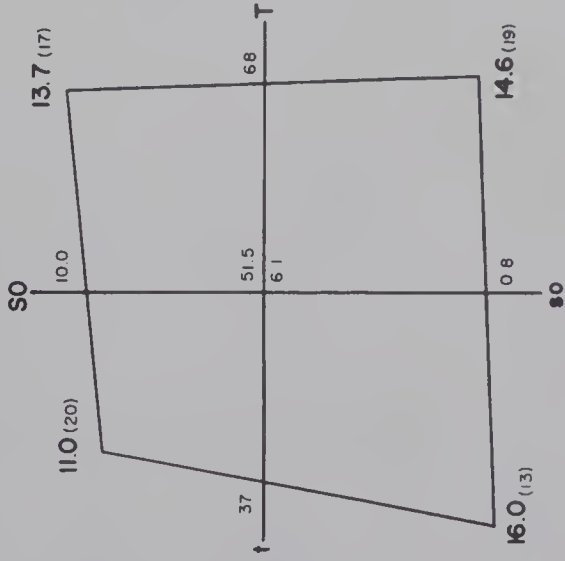
Purple martin activity at the nest entrance during the arrival, nest building and nest completion stages of the breeding cycle as influenced by the three factors: temperature, sky opacity and wind velocity.

Numbers in bold type indicate the mean number of nest entrance-departures under prevailing meteorological conditions in specific quadrants of the graph. They also represent the distance in arbitrary units from the origin along a line at 45° to the major axes. They form the corners of the polygons. Numbers in fine type indicate the median and range of values on the X and Y axes. Numbers in fine type and bracketed indicate sample size (number of pairs).

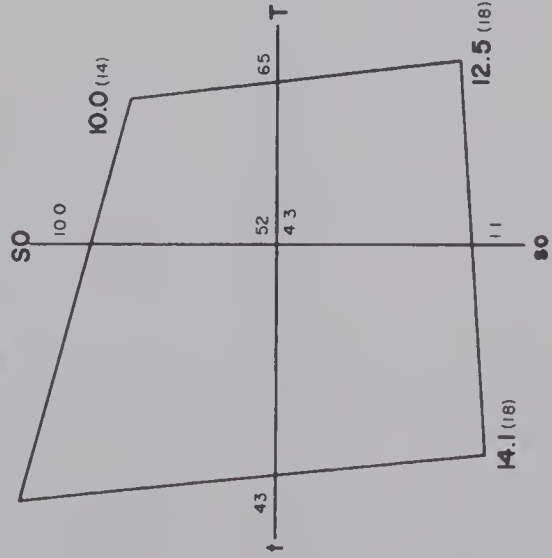
TEMPERATURE vs. SKY OPACITY vs. WIND

ARRIVAL, NEST DEFENCE, and PAIR-BOND FORMATION STAGE

Winds above 6.5 mph

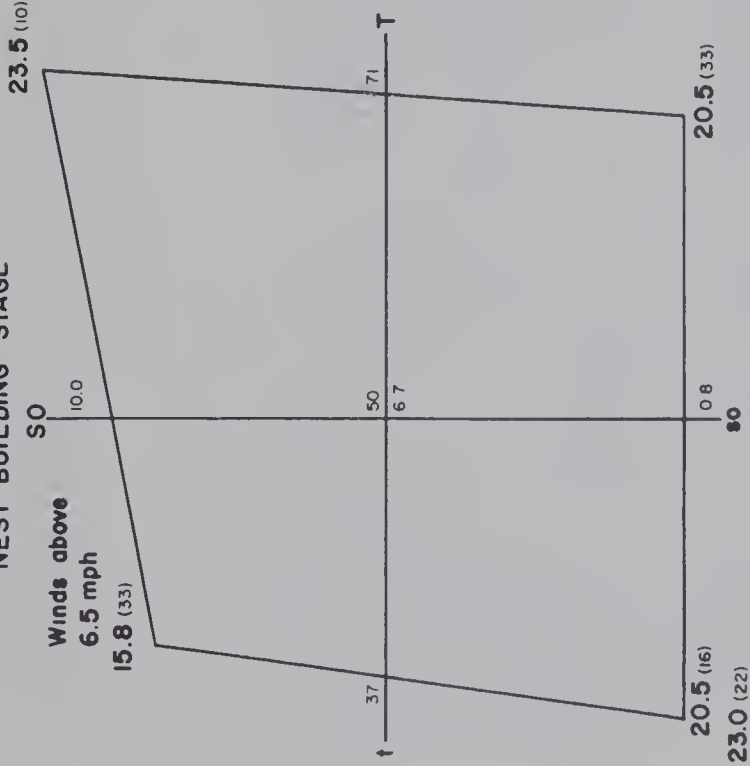


Winds below 6.5 mph

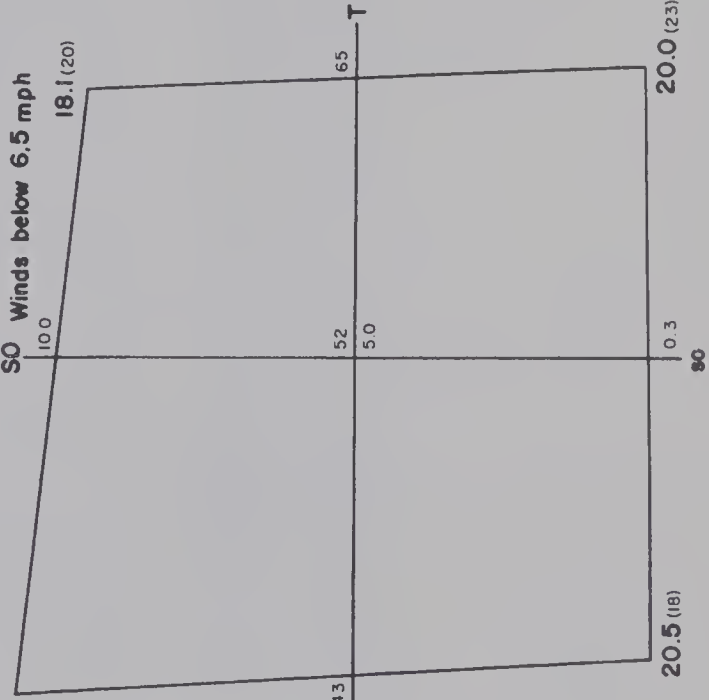


NEST BUILDING STAGE

Winds above 6.5 mph

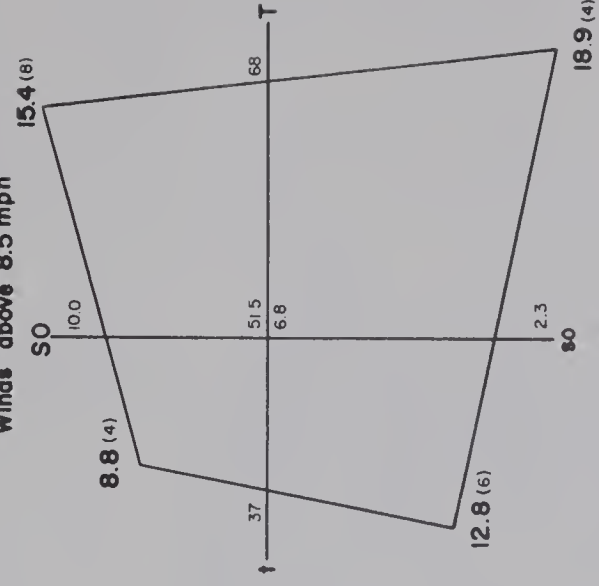


Winds below 6.5 mph

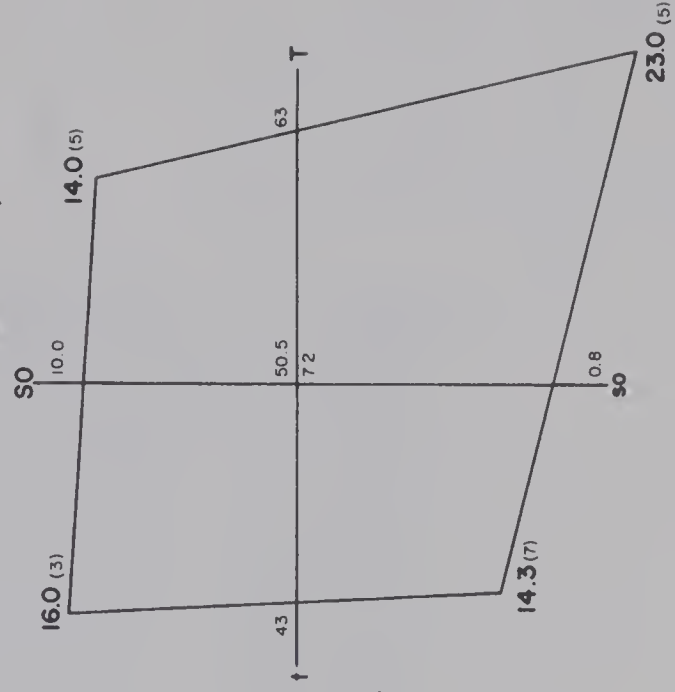


NEST COMPLETION STAGE

Winds above 8.5 mph



Winds below 8.5 mph

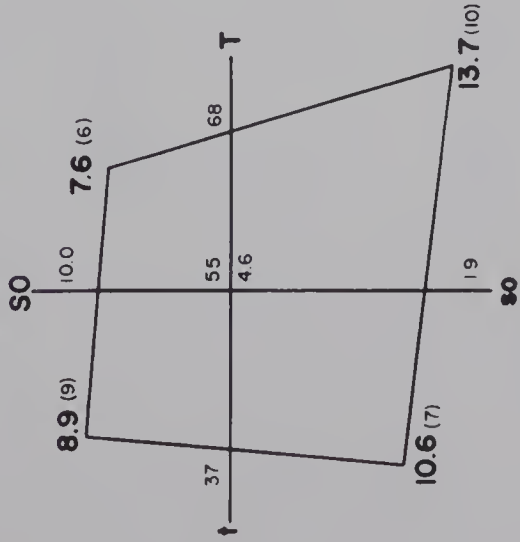


Purple martin activity at the nest entrance during the laying, incubation, nestling and post-breeding stages of the breeding cycle as influenced by the three factors: temperature, sky opacity and wind velocity.

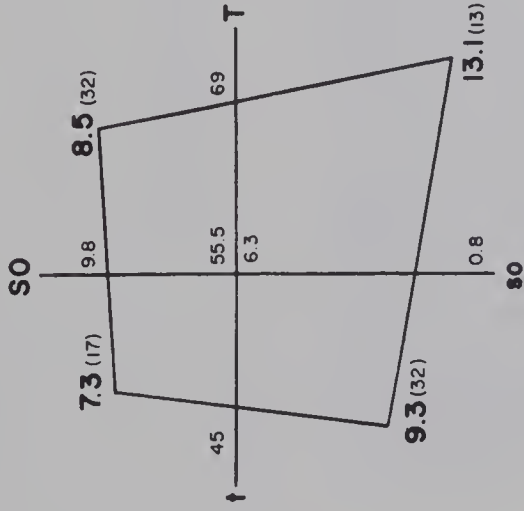
Numbers in bold type indicate the mean number of nest entrance-departures (except for the nestling stage when these numbers represent the mean of the differences from the "ideal" feeding curve as discussed in the text) under prevailing meteorological conditions in specific quadrants of the graph. They also represent the distance in arbitrary units from the origin and along a line at 45° to the major axes. They form the corners of the polygons. Numbers in fine type indicate the median and range of values on the X and Y axes. Numbers in fine type and bracketed indicate sample size (number of pairs).

TEMPERATURE vs. SKY OPACITY vs. WIND

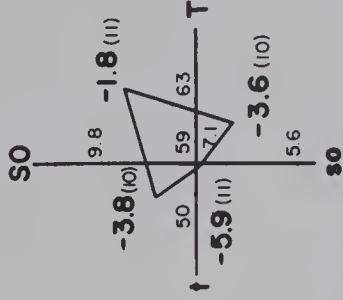
LAYING STAGE
Wind above 9.2 mph



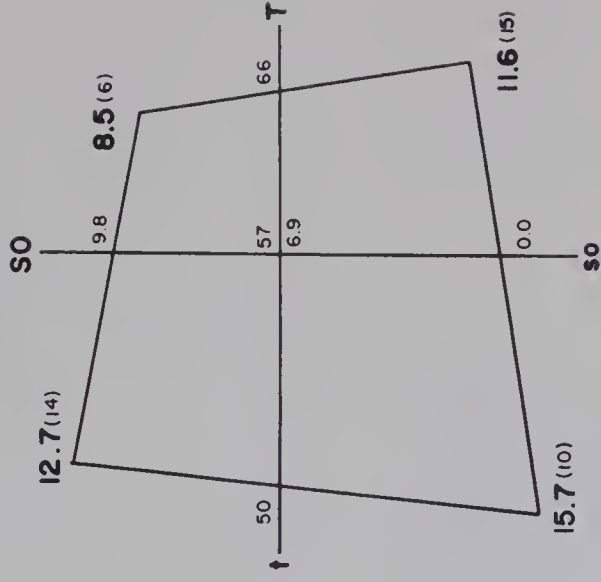
INCUBATION STAGE
Wind above 6.5 mph



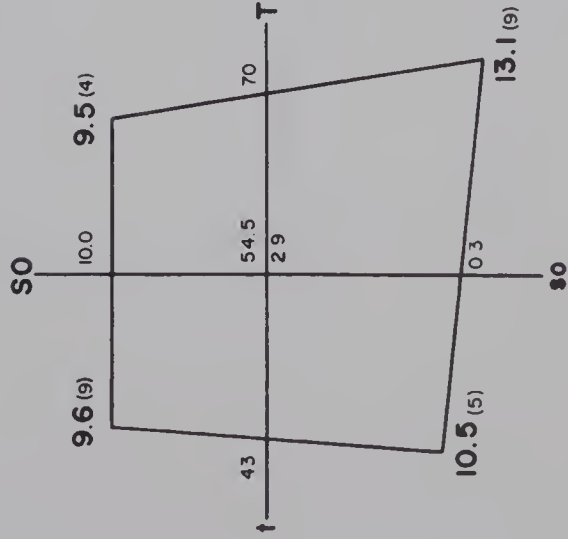
NESTLING STAGE
Wind above 6.5 mph



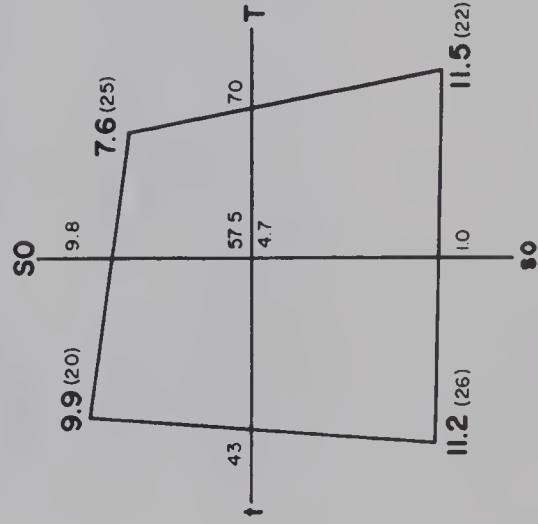
POST-BREEDING STAGE
Wind above 5.5 mph



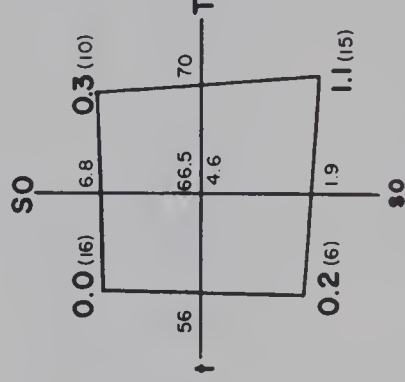
Wind below 9.2 mph



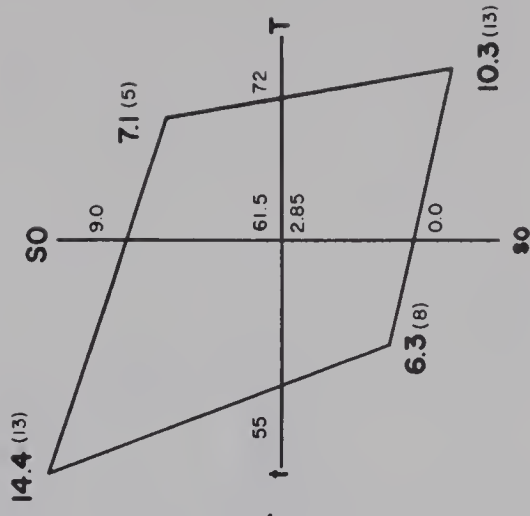
Wind below 6.5 mph



Wind below 6.5 mph



Wind below 5.5 mph



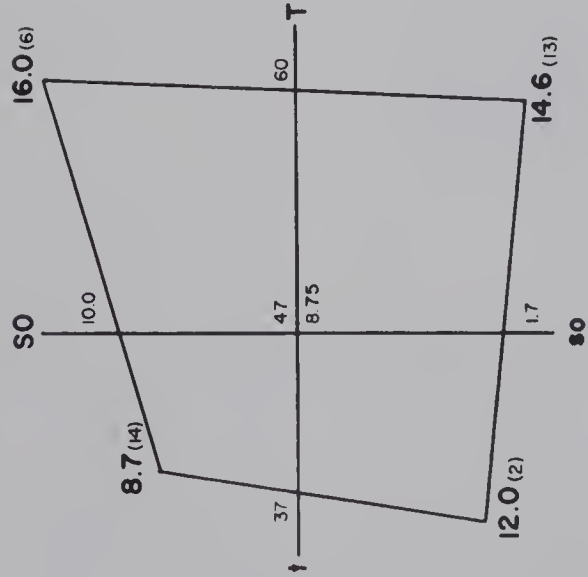
Appendix XV.

Purple martin activity at the nest entrance during the arrival, nest defence, pair-bond formation stage as influenced by four factors: temperature, sky opacity, wind velocity and relative humidity.

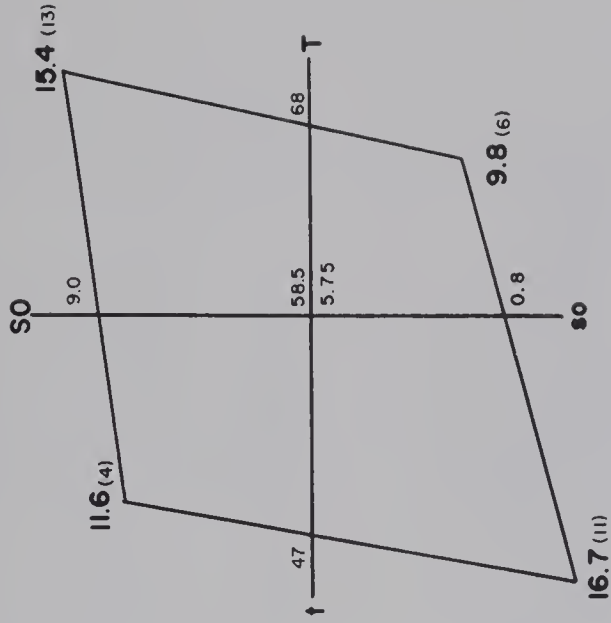
Numbers in bold type indicate the mean number of nest entrance-departures under prevailing meteorological conditions in specific quadrants of the graph. They also represent the distance in arbitrary units from the origin and along a line at 45° to the major axes. They form the corners of the polygons. Numbers in fine type indicate the median and range of values on the X and Y axes. Numbers in fine type and bracketed indicate sample size (number of pairs).

TEMPERATURE vs. SKY OPACITY vs. WIND vs. RELATIVE HUMIDITY

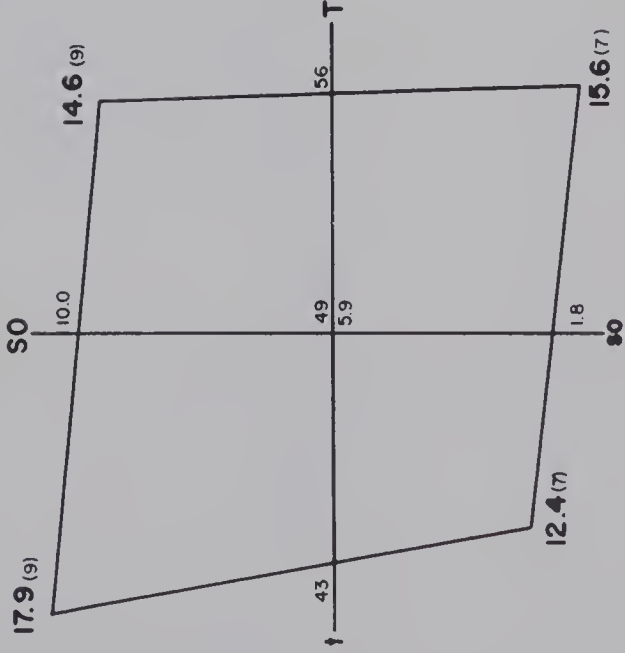
ARRIVAL, NEST DEFENCE, PAIR-BOND FORMATION STAGE



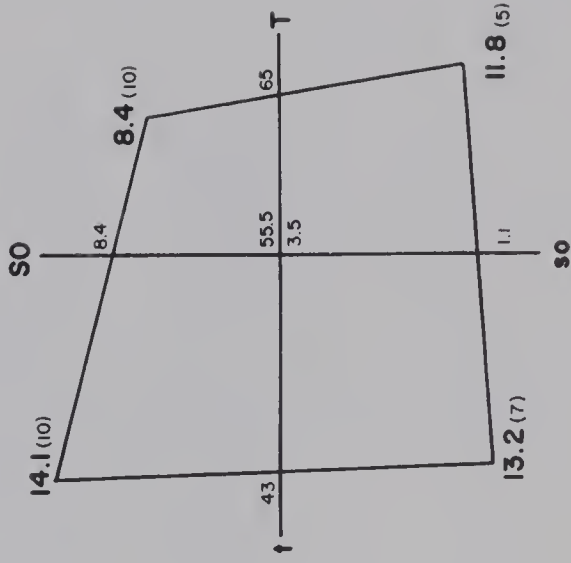
Wind above 6.5 mph



Relative humidity above 62 %



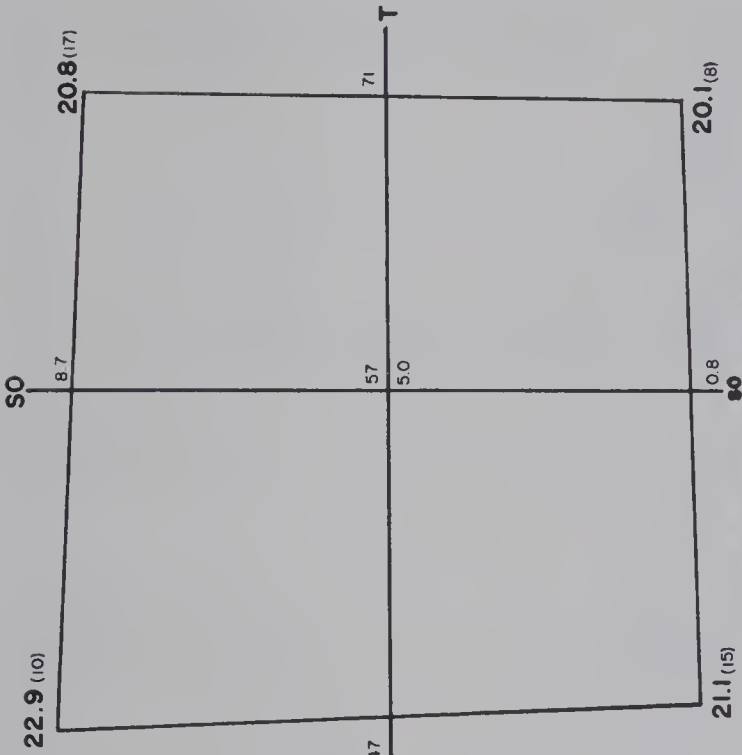
Wind below 6.5 mph



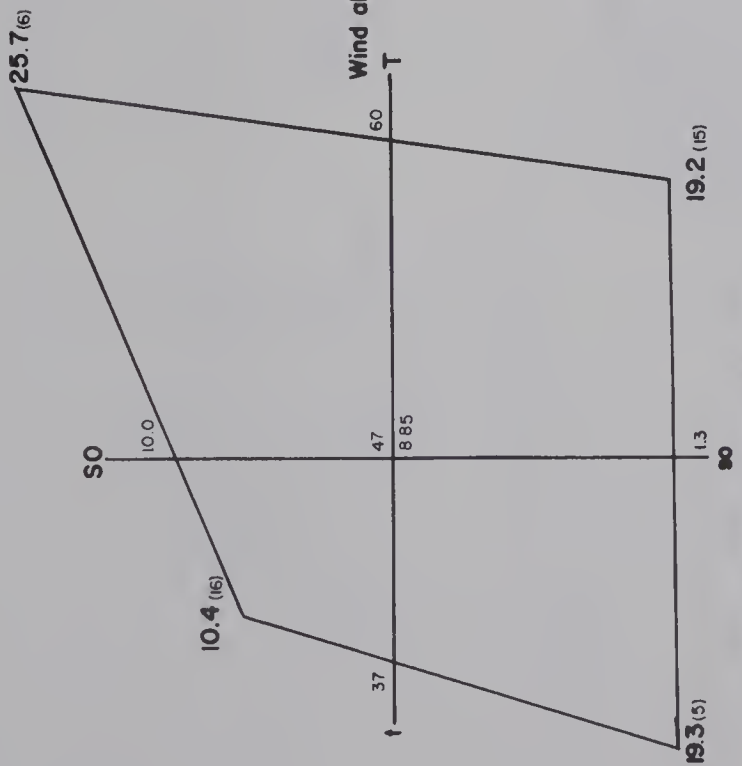
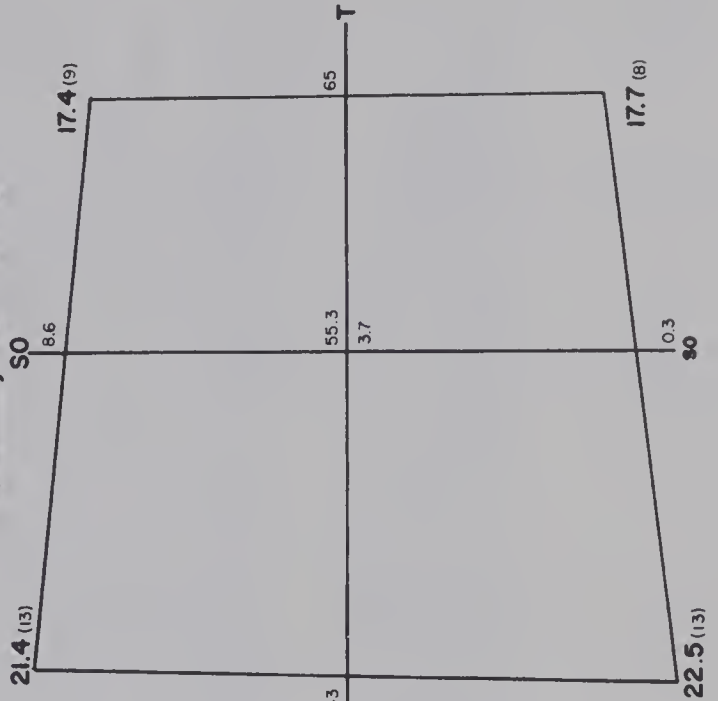
Appendix XVI. Purple martin activity at the nest entrance during the nest building stage as influenced by four factors: temperature, sky opacity, wind velocity and relative humidity.

Numbers in bold type indicate the mean number of nest entrance-departures under prevailing meteorological conditions in specific quadrants of the graph. They also represent the distance in arbitrary units from the origin along a line at 45° to the major axes. They form the corners of the polygons. Numbers in fine type indicate the median and range of values on the X and Y axes. Numbers in fine type and bracketed indicate sample size (number of pairs).

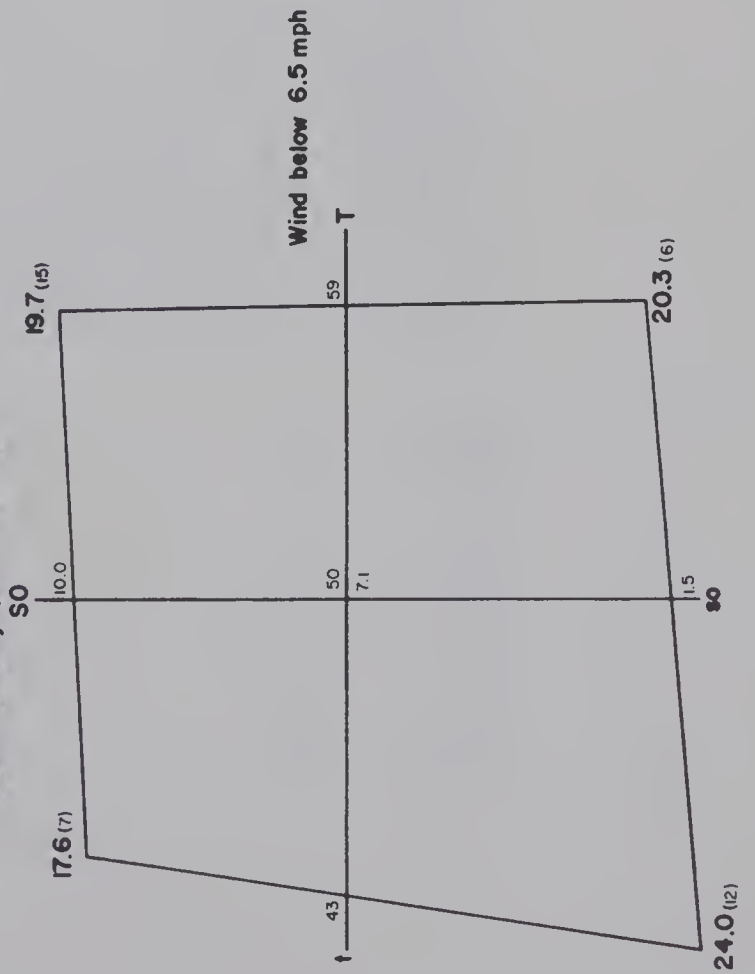
TEMPERATURE vs. SKY OPACITY vs. WIND vs. RELATIVE HUMIDITY
NEST BUILDING STAGE



Relative humidity below 64.5 %



Relative humidity above 64.5 %

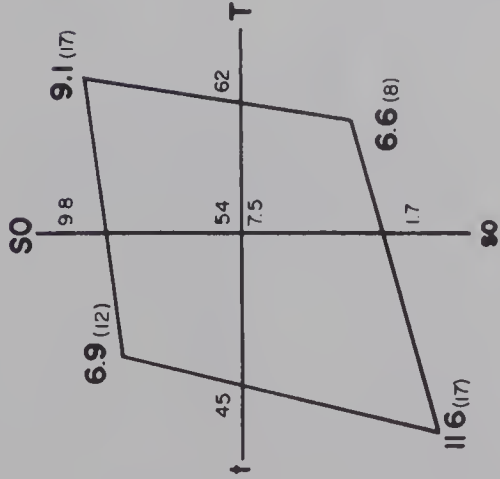


Purple martin activity at the nest entrance during the incubation stage as influenced by four factors: temperature, sky opacity, wind velocity and relative humidity.

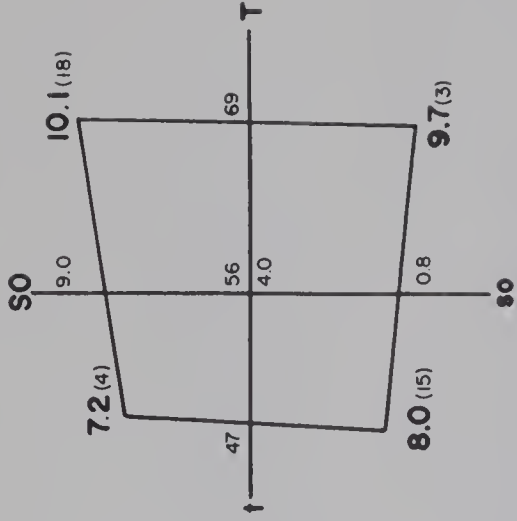
Numbers in bold type indicate the mean number of nest entrance-departures under prevailing meteorological conditions in specific quadrants of the graph. They also represent the distance in arbitrary units from the origin along a line at 45° to the major axes. They form the corners of the polygons. Numbers in fine type indicate the median and range of values on the X and Y axes. Numbers in fine type and bracketed indicate sample size (number of pairs).

TEMPERATURE vs. SKY OPACITY vs. WIND vs. RELATIVE HUMIDITY

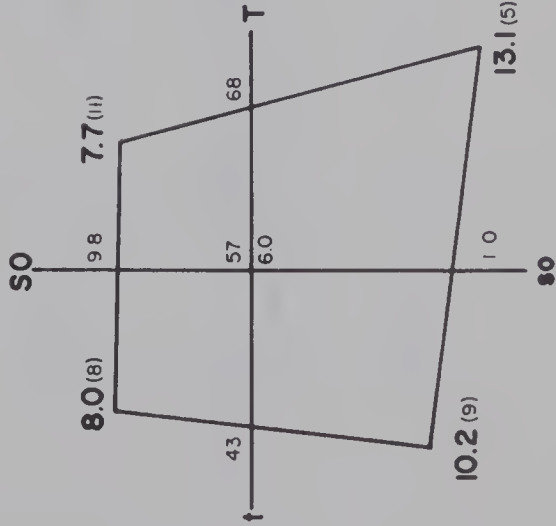
INCUBATION STAGE



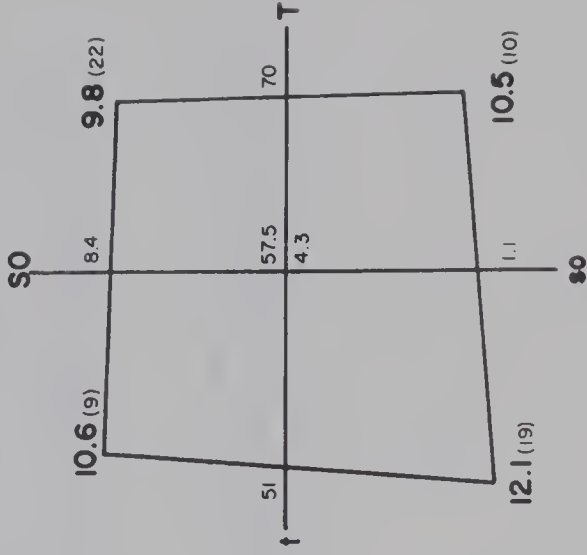
Wind above 6.5 mph



Relative humidity above 60.5 %



Wind below 6.5 mph



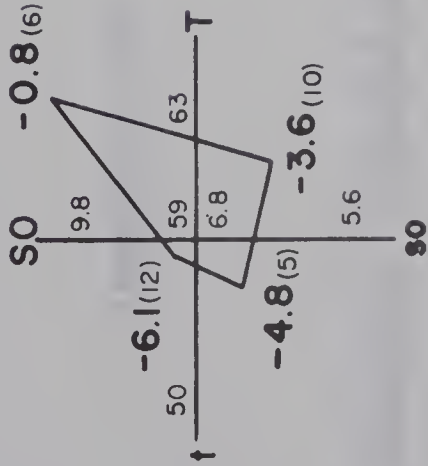
Relative humidity below 60.5 %

Appendix XVIII. Purple martin activity at the nest entrance during the nestling stage as influenced by four factors: temperature, sky opacity, relative humidity, and wind velocity.

Numbers in bold type represent the mean of the differences from the "ideal" feeding curve, as discussed in the text, under prevailing meteorological conditions in specific quadrants of the graph. They also represent the distance in arbitrary units from the origin along a line at 45° to the major axes. They form the corners of the polygons. Numbers in fine type indicate the median and range of values on the X and Y axes. Numbers in fine type and bracketed indicate sample size (number of pairs).

TEMPERATURE vs. SKY OPACITY vs. RELATIVE HUMIDITY vs. WIND

NESTLING STAGE

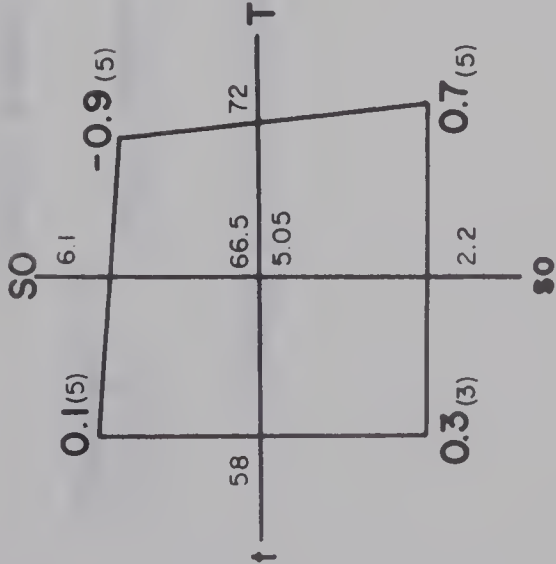


Wind above 6.5 mph

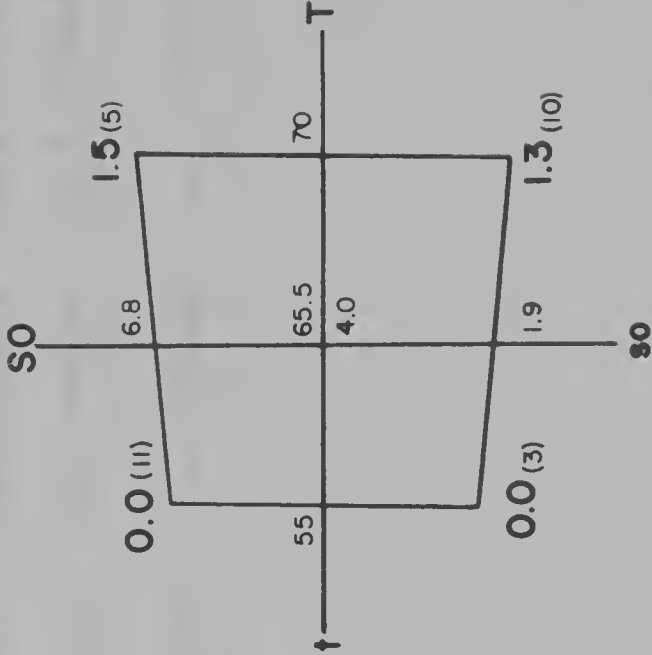
Insufficient data

Relative humidity above 64.5 %

Relative humidity below 64.5 %



Wind below 6.5 mph



Appendix XIX. Measurements of adult purple martins from the
 Edmonton area compared to birds in the
 Eastern U.S.A. Measurements made according
 to Pettingill (1961) and are presented in
 millimeters.

<u>Location</u>	<u>Sex and age</u>	<u>Sample size</u>	<u>Wind chord</u>		<u>Tail</u>		<u>Tarsus</u>		<u>Bill</u>	
			<u>Mean</u>	<u>Range</u>	<u>Mean</u>	<u>Range</u>	<u>Mean</u>	<u>Range</u>	<u>Mean</u>	<u>Range</u>
Edmonton	Male (adult and yearling)	15	152.5	145-161	76.5	71-91	15.9	14-18	11.4	10-12
	Female	19	150	143-157	71.2	66-78	15.5	13-18	11.4	10-13
	Both sexes	34	151.1	143-161	73.7	66-91	15.7	13-18	11.4	10-13
Eastern * U.S.A.	Both sexes	--	--	129-157	--	70-88	--	11-16	--	11-13

* Data from Forbush (1929)

B29892